Cultural Neuroscience: Biology of the Mind in Cultural Contexts

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Abstract

This article provides a review of how cultural contexts shape and are shaped by psychological and neurobiological processes. We propose a framework that aims to culturally contextualize behavioral, genetic, neural, and physiological processes. Empirical evidence is presented to offer concrete examples of how neurobiological processes underlie social behaviors, and how these components are interconnected in larger cultural contexts. These findings provide some understanding of how the meanings shared by cultural experiences trigger a neurobiological, psychological, and behavioral chain of events, and how these events may be coordinated and maintained within a person. The review concludes with a reflection on the current state of cultural neuroscience and questions for the field to address.

Contents

INTRODUCTION 24.2
FRAMEWORK OF CULTURAL NEUROSCIENCE 24.3
GENETICS 24.4
The Theory of Dual Inheritance, or Gene-Culture Coevolution 24.4
Gene-Environment Interaction 24.5
Gene-Culture Interaction 24.5
NEURAL CORRELATES AND STRUCTURAL CHANGE 24.11
Representations of Self Versus Others 24.11
Cognitive Processes 24.12
Emotions and Interpersonal and Group Processes 24.14
Neuroanatomical Differences 24.15
PHYSIOLOGICAL PROCESSES 24.16
Social Relationships 24.16
Cognitive and Emotional Processes 24.17
Neurotransmitters and Social Behaviors 24.18
INTEGRATION AND FUTURE DIRECTIONS OF CULTURAL NEUROSCIENCE 24.19

INTRODUCTION

At the root of the study of the mind and behavior has always been the question of nature and nurture. Some previous philosophical and scientific inquiries have taken the view that the human mind and its contents are almost entirely acquired (Aristotle and Locke) or almost entirely innate (Plato and Hobbes), and hence, the phrase "nature versus nurture" was coined (Galton 1874). Most contemporary researchers, however, acknowledge both nature and nurture as joint determinants that influence psychological and behavioral outcomes (Plomin & Asbury 2005). Thus, the more productive questions for current scientific inquiries should be, How do nature and nurture work together, and what are the processes through which biology and culture shape the mind?

Cultural psychology is a field that investigates the influence of nurture, or cultural contexts, on human psychological tendencies and behaviors (Fiske et al. 1998, Shweder 1995). Over the last few decades, the field has generated numerous empirical findings that highlight diversity in human behaviors, traits, and psychological processes as products of engagement in specific sociocultural contexts. The specific nature of culture is multidimensional in that it includes shared physical environments, social structures, institutions, interactions, worldviews, and values (Kitayama et al. 1997, Kim & Markus 1999, Miyamoto et al. 2006). Cultural contexts are made up of these products of human minds that are loosely but coherently built on shared basic assumptions about the world (Kitayama 2002). They provide a shared meaning system through which individuals interpret situations and make sense of their experiences, and these meanings that are shared within cultural contexts are at the psychological core of nurture (Bruner 1990).

Although the empirical focus of cultural psychology has been on nurture, researchers recognize that in humans the impact of nature, or biological processes and constraints, at both species and individual levels, should not be ignored and that it is imperative to look at how nature and nurture jointly make up human psychological and behavioral tendencies. The recent emergence of cultural neuroscience attests to such recognition. Cultural neuroscience is a branch of cultural psychology

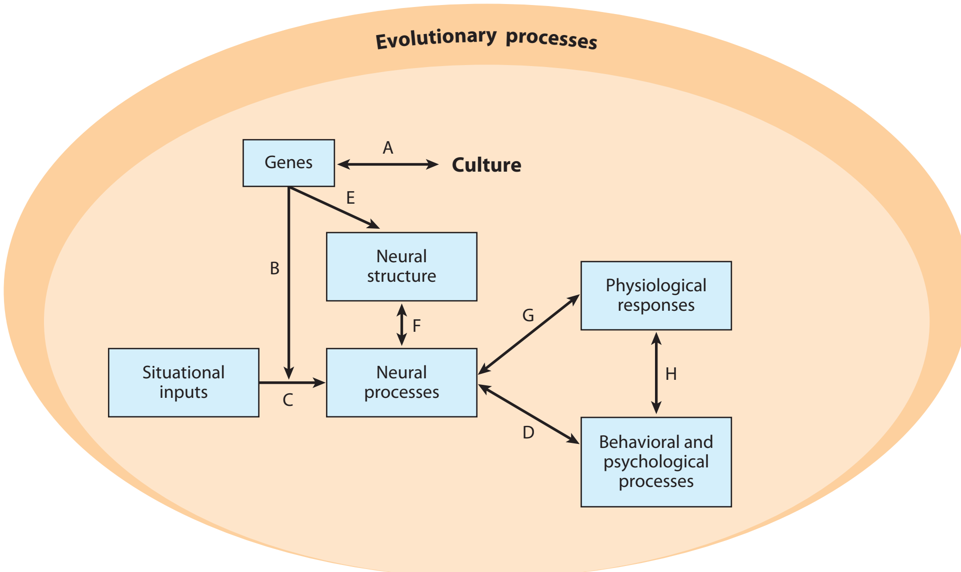

Figure 1

Framework of cultural neuroscience.

that aims to address how cultural and biological factors interact (Chiao & Ambady 2007). It is perhaps an unexpected combination of perspectives—the study of meaning and the study of the neural system—but it is a combination that is essential to gain a fuller understanding of human behaviors and psychological processes. This review focuses on how shared meanings afforded by cultural contexts shape and are shaped by psychological and biological processes.

FRAMEWORK OF CULTURAL NEUROSCIENCE

The field of cultural psychology has flourished and accumulated a large body of literature over the last several decades. Although these empirical investigations began with comparisons between national/ethnic cultures, they later became more inclusive of other sociocultural contexts, such as social class (Snibbe & Markus 2005, Stephens et al. 2007), regions within a country (Kitayama et al. 2006a, Nisbett 1993, Uskul et al. 2008), and religion (Cohen & Hill 2007, Tsai et al. 2007; see Cohen 2009 for a review). In terms of the domains of psychology, researchers have documented cultural variations in just about every aspect of psychological functioning, from the more basic processes, such as emotion (Kitayama et al. 2006b) and cognition (Nisbett et al. 2001) to more complex processes, such as the self (Heine et al. 1999), relationships (Kim et al. 2008), and psychological well-being (Suh 2002).

In this review, we present findings regarding how cultural factors are linked to neurobiological functioning and propose an overarching framework of cultural neuroscience that is inclusive of different levels of analysis (**Figure 1**). The central argument of our framework is that individuals' biological and psychological processes occur within larger cultural contexts and the constraints of evolutionary processes. At present, the existing empirical evidence illuminating these interlocking processes is relatively limited, and some processes, especially the ways in which different levels implicate each other, have yet to be empirically studied. However, it is worthwhile to consider how these biological components work together and are influenced by cultural contexts.

In this review, we present existing evidence in three broad sections to provide concrete examples of how these biological processes occur in larger cultural contexts. The next section, on "Genetics," reviews theories and empirical evidence on how cultural and genetic factors influence each other at a larger societal level through evolutionary processes via gene-culture coevolution (Link A in **Figure 1**) as well as theories and evidence on how cultural factors and genetic factors interact to shape individuals' psychological and behavioral tendencies via gene-culture interaction (Links B → C → D). We speculate that these interactions between genes and culture exist because genes and cultural meanings shape people's interpretation of situations, which in turn implicates psychological and behavioral outcomes via neural structures and responses. The section on "Neural Correlates and Structural Change" addresses neural structures and activity underlying psychological processes primarily by reviewing brain imaging and electroencephalography (EEG) studies. In this section, we discuss how cultural factors influence the way the brain processes information and how the results corroborate cultural differences in behavioral and psychological outcomes (Links C and D). We also review evidence on the cultural shaping of brain structure. We speculate that this occurs through the interaction of genes and culture (Link E) and through culture-specific neural activities (Link F). The section on "Physiological Processes" addresses findings from studies that involve physiological responses. More specifically, we review how culture moderates cardiovascular, neuroendocrine, and immune responses to situational cues (Links C and G). We also review studies that consider these physiological responses as correlates of psychological and behavioral outcomes to speculate on their role in shaping social behaviors that contribute to the maintenance of cultures (Link H).

GENETICS

Because genes are considered one of the potential determinants of behaviors and other psychological outcomes, an important question is how genes and cultural contexts jointly affect human psychology. We argue that cultural factors may influence how genetic predispositions manifest themselves in behavioral and psychological tendencies, and we review several relevant theoretical approaches that aim to explain the possible ways in which genes and culture work together.

The Theory of Dual Inheritance, or Gene-Culture Coevolution

Dual inheritance theory (Boyd & Richerson 1985), also known as gene-culture coevolutionary theory (Chiao & Blizinsky 2010, Feldman & Laland 1996; see also Cavalli-Sforza & Feldman 1981, Fincher & Thornhill 2012, Lumsden & Wilson 1981), posits that just as the process of natural selection acts on genes to transmit genetic information from one generation to the next, cultural traits are adaptive, and cultural selection may simultaneously influence and be influenced by genetic selection. According to this theory, certain genotypes may predispose people to create particular features in their environment, thus influencing cultural selection, or the normative traits and tendencies that are culturally transmitted. Concurrently, aspects of the broader culture may act as environmental pressures that ultimately affect genetic selection, or the types of traits that are genetically selected in that culture (see Odling-Smee et al. 2003 for a discussion of the process of niche construction). By conceptualizing culture as a phenomenon that evolves in interaction with genetic selection processes, dual inheritance theory aims to explain the macrolevel interplay between genes and culture.

Numerous empirical studies have found support for the theory of dual inheritance. For example, in a study of lactose tolerance across Europe, researchers showed that cultures that depend more on milk products tend to support lactose-tolerant human populations, and the cattle in these regions tend to have higher frequencies of milk protein genes (Beja-Pereira et al. 2003). The authors argued that the human fitness advantages of milk consumption led to (*a*) selection of genes for lactose tolerance in humans, (*b*) transmission of cultural practices supporting cattle domestication and milk consumption, and (*c*) selection of milk-protein genes in cattle. The co-occurrence of these events suggests that genes and culture may influence each other in coevolution.

To bridge dual inheritance theory with perspectives from cultural psychology, researchers have studied whether prevalence of certain genotypes is associated with particular cultural tendencies. One study showed that nations with a greater historical prevalence of pathogens also tended to be more collectivistic, and this association may be explained by higher frequencies of the short (S) allele on the promoter region polymorphism (5-HTTLPR) of the serotonin transporter gene *SLC6A4* compared with the long (L) allele (Chiao & Blizinsky 2010, Way & Lieberman 2010). Moreover, although the S allele of the 5-HTTLPR polymorphism is linked to greater risk of depression, anxiety, and negative affect at the individual level (Lesch et al. 1996), there is an inverse correlation between the frequency of the S allele and the rate of anxiety and depression at the national level. Given that the cultural value of collectivism may buffer against threats such as pathogen prevalence (Fincher et al. 2008), collectivism may also serve the adaptive function of reducing the risk of environmental stress, which may have led to genetic selection of the S allele of 5-HTTLPR in collectivistic cultures (Chiao & Blizinsky 2010; see also Chiao 2010).

Gene-Environment Interaction

Another model that offers an understanding of how genetic factors influence psychological outcomes of individuals is that of gene-environment interaction. This model theorizes not that genes relate to outcomes directly but rather that genetic influences may be moderated by environmental input (Caspi et al. 2002, 2003). Some people may be genetically predisposed to react to a given environmental influence more strongly than others, and likewise, people with the same genetic predisposition may at times react quite differently depending on differences in the environment. For instance, a study by Caspi et al. (2003) found that the association between adverse life events and degree of depressive symptoms is much stronger among those who carry an S allele of the 5-HTTLPR polymorphism than in those who do not (see Karg et al. 2011 for meta-analytic support for this gene-environment interaction). Gene-environment interactions have also been observed with other genes, such as the dopamine D4 receptor (*DRD4*) gene (Bakermans-Kranenburg et al. 2008, Sasaki et al. 2013) and the monoamine oxidase-A (*MAOA*) gene (Caspi et al. 2002).

Although these previous studies suggest that certain risk genotypes lead to greater vulnerability to negative experiences, further studies showed that they may also be associated with increased benefits from positive social environments (Taylor et al. 2006). Thus, it has been suggested that, rather than genetic risk, these genetic influences may be more accurately described as susceptibility to environmental influence (Belsky et al. 2009, Obradović & Boyce 2009, Way & Taylor 2010). The notion of differential susceptibility allows multiple ways of conceptualizing the nature of environment as well as different outcome variables that are implicated in gene-environment interactions. One such framework stemming from this notion is that of gene-culture interaction.

Gene-Culture Interaction

The gene-culture interaction model builds and expands on the gene-environment interaction framework. Gene-environment interaction research is mostly concerned with psychological and physical health outcomes as a way to understand factors that make people vulnerable to health-related risks. Consequently, this research tends to focus on the environment as a factor that varies in the degree to which it causes distress or provides support to individuals. The gene-culture interaction model includes cultural contexts in the notion of environment. Culture differs from the typical conceptualization of environment in at least two ways. First, culture is a form of the environment within which a certain set of loosely but coherently connected values, institutions, and patterns of actions and interactions are collectively shared (Kitayama 2002). Thus, gene-culture-interaction studies operationalize the cultural environment as social groups with shared experiences—such as national or regional culture, religion, and social class—that shape specific meaning systems. Second, because divergences across cultures reflect each group's adaptation to their context-specific challenges and goals, the gene-culture interaction model assumes cultural tendencies to be comparably functional within their own contexts and supports investigation of patterns of normative behaviors and psychological tendencies in addition to well-being and health-related outcomes.

The gene-culture interaction model also differs from dual inheritance theory. Dual inheritance theory provides a theoretical framework to understand the macroevolutionary processes involving culture and genes, and thus it is not conceived as a way to explain the process in which genetic and sociocultural factors interact to shape psychological tendencies and behaviors at the individual level (Kim & Sasaki 2012). The gene-culture interaction model posits that there is a genetic basis for the susceptibility to environmental input, and thus the degree to which one engages in culture-specific behaviors may be influenced by these genetic factors. In other words, dual inheritance theory concerns the distribution of specific genes within cultural groups, whereas the gene-culture interaction model concerns culturally moderated associations between specific genes and behavioral and psychological tendencies (Sasaki 2013).

From the gene-culture interaction perspective, genetic influences shape psychological and behavioral predispositions, and cultural influences may shape how these predispositions are manifested in social behaviors and psychological outcomes. Below we review empirical findings that support the model, drawing on evidence from a range of psychological processes, from attention to psychological well-being. A basic assumption in all these studies is that certain genes are associated with the degree of sensitivity to certain aspects of environmental input, building on the idea of differential susceptibility (Belsky et al. 2009, Obradović & Boyce 2009, Way & Taylor 2010). The model predicts that particular genotypes predispose the carriers to respond particularly strongly to environmental input. Thus, when these carriers are engaged in different cultural contexts with divergent patterns and meanings of psychological and behavioral tendencies, they should embody those specific patterns that are expected and rewarded in their respective cultural contexts more closely compared with those who do not carry the same genotypes (Kim & Sasaki 2012). Consequently, the model also predicts that carrying these differential susceptibility genes could at times lead to different and even opposite behavioral outcomes in different cultures.

Cognitive processes. A study of locus of attention examined a serotonin receptor polymorphism and culture as potential interacting determinants of this cognitive tendency (Kim et al. 2010b). Much research has found that the serotonin (5-hydroxytryptamine, or 5-HT) system is involved with several cognitive functions, and in a state of depleted serotonin, people are better able to attend to focal objects (see Schmitt et al. 2006 for a review). In addition, reliable differences have been found in locus of attention between East Asians and North Americans. Whereas Easterners tend to pay greater attention to background and contextual information, Westerners tend to pay greater attention to focal information (Masuda & Nisbett 2001). Thus, we investigated whether the link between attention and serotonin is moderated by cultural factors. We chose a polymorphism (C-1019G) within the promoter region of the serotonin receptor gene *HTR1A* as the target gene in this study and compared the cognitive styles of Koreans and European Americans.

The results showed a significant interaction between the *HTR1A* genotype and culture. Among European Americans, there was a linear pattern such that those homozygous for the guanine (G) allele (which has been previously linked with reduced serotonergic neurotransmission) reported paying less attention to nonfocal contextual information than those homozygous for the cytosine (C) allele, with those heterozygous reporting an intermediate level of attention. However, this link between *HTR1A* and locus of attention was completely reversed among Koreans: those homozygous for the G allele reported paying more attention to contextual information than those homozygous for the C allele. To help rule out the potential alternative explanation of a gene-gene interaction (Kaufman et al. 2006), or the interaction between the target gene and other unmeasured genes that covary between the two cultural groups, this study used the triangulation method. Specifically, we also included a group of Korean Americans who were born and raised in the United States and thus share a similar genetic composition with their counterparts who were born and raised in Korea but share similar cultural experiences with European Americans. The results showed that the association between *HTR1A* and locus of attention among Korean Americans was the same as that of European Americans but not that of Koreans born and raised in Korea, further supporting the conclusion that the demonstrated interaction was due to cultural factors (Kim et al. 2010b).

Another study used the model of gene-culture interaction with another serotonin system polymorphism, 5-HTTLPR, by investigating cultural differences in perceiving changes in facial expressions and whether 5-HTTLPR modulates these cultural differences (K. Ishii, H.S. Kim, J.Y. Sasaki, M. Shinada, I. Kusumi, unpublished manuscript). In a previous study, Japanese and Americans watched videos of faces with disappearing smiles (i.e., a happy expression gradually morphing into a neutral expression) and judged the point at which the emotional expressions disappeared. Japanese detected the disappearance of smiles more quickly than Americans. The authors maintained that this is because social disapproval carries greater psychological importance in Japanese culture (Ishii et al. 2011). Building on this previous finding, a gene-culture interaction study found that Japanese with the SS genotype, which is theorized to be linked to greater susceptibility to environmental input, detected the disappearance of smiles with greater perceptual efficiency, closely embodying the predominant cultural tendency, compared with Japanese with SL and LL genotypes, whereas Americans did not differ by genotype (K. Ishii, H.S. Kim, J.Y. Sasaki, M. Shinada, I. Kusumi, unpublished manuscript). As in the study described above, Asian Americans who were born and raised in the United States showed a pattern consistent with that of European Americans, whereas the Japanese (those born and raised in Japan) pattern differed from both groups. These results showed that the 5-HTTLPR polymorphism interacts with cultural factors to affect the perception of facial expressions, and those with greater environmental susceptibility seem to heighten their vigilance for culturally emphasized aspects of social cues.

Further evidence in support of the gene-culture interaction model comes from quantitative behavioral genetics. For instance, Turkheimer et al. (2003) examined the heritability of IQ as a function of social class and, interestingly, found that IQ heritability rates were much lower among families from the lowest social class compared with higher social classes. Other studies with large samples of twins (Harden et al. 2007, Tucker-Drob et al. 2011) also showed that genetic influences were significantly weaker among participants from the lowest social class. Social class provides social and physical contexts in which a meaningful degree of shared social experiences occur. Belonging to a particular social class drastically increases one's chances of engaging in a particular set of behaviors and encountering certain physical and social environments that have important implications for behavioral, psychological, and health outcomes (Schreier & Chen 2013). Thus, it appears that people from the lowest social class may come from an impoverished environment that restricts development of genetic potential (see Nisbett et al. 2012 for a review).

Emotional processes. The tendency to suppress one's feelings is an emotion regulation strategy that is more common in East Asian cultures than in the United States (Matsumoto et al. 2008, Tsai & Levenson 1997). In the United States, expression of emotion is encouraged more strongly (Butler et al. 2009, Kim & Chu 2011). Based on these behavioral differences, we conducted a gene-culture interaction study in which Korean and American participants indicated their tendency to regulate their emotions using suppression, and we determined their genotype for an oxytocin receptor gene (*OXTR rs*53576) (Kim et al. 2011). The G allele of *OXTR rs*53576 is associated with more sensitive parenting behavior (Bakermans-Kranenburg & Van IJzendoorn 2008), greater sensitivity to infant crying (Riem et al. 2011), more empathic accuracy (Rodrigues et al. 2009), and less loneliness (Lucht et al. 2009) compared with the adenine (A) allele. The results of this study showed the expected interaction between culture and *OXTR* (Kim et al. 2011). Americans with two copies of the G allele (GG genotype, which has been linked to greater socioemotional sensitivity) reported suppressing emotion significantly less than Americans with two copies of the A allele (AA genotype, which has been linked to less socioemotional sensitivity), consistent with the idea that *less* emotional suppression may be the more emotionally sensitive response in mainstream American culture. However, Koreans showed the exact opposite pattern: Those with the GG genotype reported suppressing emotion *more* than those with the AA genotype, which supports past research suggesting that emotional suppression may be the more emotionally sensitive response in East Asian culture. The analysis including Asian Americans who were born and raised in the United States for triangulation purposes, again, showed that the Asian American pattern of association was more similar to that of European Americans than it was to that of Koreans born and raised in Korea.

Interpersonal and prosocial behaviors. To investigate the gene-culture interaction in a more interpersonal domain, we examined the roles of culture and *OXTR rs*53576 in the use of emotional support (Kim et al. 2010a). Previous research has shown that cultures differ in the norms and evaluations of emotional support seeking as a means for coping with stress and that Asians tend to be more cautious than European Americans about seeking support from close others (Kim et al. 2008). Building on these findings, we conducted a study in which Koreans and Americans, including Korean Americans and European Americans who were born and raised in the United States, indicated their current distress level and their social support seeking behaviors. Results again supported the gene-culture interaction model. The relationship between *OXTR* and emotional support seeking was moderated by both culture and distress level. In particular, when under great distress, Americans with either GG or AG genotypes reported relying on emotional support more than Americans with the AA genotype. In contrast, Koreans with GG or AG genotypes did not increase support seeking any more than those with the AA genotype. The same triangulation as used in previously described studies confirmed that for Korean Americans, although the overall level of emotional support seeking was in the middle of the levels of European Americans and Koreans, the pattern of association between OXTR genotypes and emotional support seeking was very similar to that of European Americans but not to that of Koreans. These results, again, show that people with genotypes that are expected to render them more sensitive to the social environment seem to be more strongly influenced by sociocultural expectations than are people without those genotypes.

Taking a somewhat different approach, another study examined how implicit priming of religion would moderate the association between *DRD4* and prosocial behaviors (Sasaki et al. 2013). This study differs from other studies examining the interaction between a gene and sociocultural context in that it incorporated experimental priming of religious thoughts. Certain *DRD4* variants (7-repeat or 2-repeat alleles, depending on ethnicity; Wang et al. 2004) are expected to be associated with greater susceptibility to reward- and punishment-related environmental influences than others. Thus, we theorized that carriers of these alleles would be more susceptible to environmentally triggered religious thoughts that typically encourage prosocial behaviors (Shariff & Norenzayan 2007). Indeed, participants with *DRD4* susceptibility variants behaved in a more prosocial manner when implicitly primed with religious concepts compared with the control condition, whereas participants without *DRD4* susceptibility variants were not affected by priming. This study directly tested the idea of environmental susceptibility, and the findings support a few notable inferences. First, the differential susceptibility gene may influence even how one is affected by fleeting situational cues, such as implicit primes, not just long-term development and socialization. Second, this study demonstrated the directionality of environmental influence. Taken together with the other gene-culture interaction studies, this research suggests that carriers of differential susceptibility genes tend to assimilate to what is expected and fostered by the environment in a systematic way.

Well-being and health. Much research has demonstrated the importance of sociocultural contexts in how given psychological experiences lead to different well-being outcomes (Kitayama et al. 2006b, Suh 2002). Gene-culture interaction findings suggest that genetic factors, in conjunction with sociocultural factors, may also play a role in shaping one's well-being. In fact, Dressler and colleagues (2009) found that, in Brazil, cultural consonance—the extent to which people perceive their family's values as congruent with the values of one's culture—interacted with a serotonin receptor polymorphism (*HTR2A* −1438G-A) in influencing depressive symptoms. Although this study was conducted in the context of a single culture, this finding suggests the psychological importance of the subjective sense that one's life is culturally normative, especially for people with a greater-susceptibility genotype.

In related research, we examined how cultural factors and genetic factors may jointly affect people's psychological well-being, specifically looking at the roles of regional culture, religiosity, and *OXTR*. Previous research has investigated the link between religiosity and psychological and physical well-being and found that the link is generally, but not always, positive (McCullough et al. 2000). One of the ways that religion may benefit individuals is by increasing social affiliation, such as involvement in a fellowship or community (Atran & Norenzayan 2004). Although this may be true universally, the degree to which a religion emphasizes the importance of social affiliation may differ by culture: Religion in an East Asian cultural context tends to place greater emphasis on social affiliation than religion in a North American cultural context (Sasaki & Kim 2011). Given that some individuals may be genetically predisposed to be more socially sensitive than others, the way religion is linked to well-being may depend on cultural context and genetic makeup. A gene-culture interaction study found that Koreans showed a positive relationship between religiosity and psychological well-being, whereas European Americans showed a negative relationship, but these relationships between religiosity and well-being were found only among people who were more genetically predisposed to social sensitivity (i.e., those with an *OXTR* genotype of GG). Interestingly, there was no cultural difference in the relationship between religiosity and psychological well-being for people with other *OXTR* genotypes, who were less genetically predisposed toward social sensitivity. In fact, for people with *OXTR* genotypes associated with less social sensitivity, there seemed to be no relationship between religiosity and well-being, regardless of culture. Thus, although social affiliation may be an important part of religion everywhere, the well-being benefits that occur through religious social affiliation may be particularly strong in certain cultures, such as in East Asia, that provide relatively greater opportunities for social affiliation in religious groups. Furthermore, this cultural difference may occur only for those who are genetically predisposed to be sensitive to social affiliative behaviors in the first place (Sasaki et al. 2011).

Other studies found that genes interact with social class to shape psychological and biological functions (Adler et al. 1994, Miller et al. 2009). To explain health discrepancies between groups, researchers have investigated biological mechanisms that may be implicated by different experiences. For example, one study found that there are detectable changes in gene transcription that occur as a result of early life experiences (Miller et al. 2009). Among people who grew up in low-social-class contexts, genes associated with proinflammatory actions were upregulated, and genes responsive to glucocorticoid receptor–mediated signaling were downregulated. This is a defensive phenotypic pattern that reflects the body's reaction to threatening environments. In particular, this pattern tends to result in heightened immune activation as well as increased cortisol output, which may increase chances of survival in the short term but have negative consequences in the long term. Thus, in addition to showing how gene expression can be moderated by sociocultural inputs, these results suggest important downstream effects on well-being outcomes, including mental and physical health.

Further thoughts on genes and culture. Research investigating the interplay of specific genes and culture in shaping individuals' psychological and behavioral tendencies is still in its infancy. However, the early empirical evidence highlights the mutual influence of genetic and sociocultural factors in shaping processes beyond health and well-being outcomes. Moreover, by examining behavioral tendencies that differ across cultural contexts, these studies point to a systematic pattern of genetic susceptibility within specific cultural contexts in that cultural influences nudge the behaviors and psychological tendencies of those with susceptibility genes in the culturally consonant direction. Moreover, the exact patterns of these interactions may be systematic and informative. In some studies, the interaction is a full crossover interaction; in other studies, the interaction is driven by a significant association in one culture and a lack of association in the other culture. For example, *OXTR* is significantly associated with emotional support seeking in the United States, where people are encouraged to seek emotional support when under distress, but this association is not significant in Korea, where such encouragement is absent. However, *OXTR* is significantly associated with emotion suppression in both Korea and the United States, but in opposite directions. This may be because not only is there a norm of emotion suppression in Korea but there is also a counter-norm of emotion expression in the United States (Butler et al. 2009, Kim & Chu 2011). Similarly, *HTR1A* is associated with locus of attention in opposite ways in Korea and the United States. Perhaps this also is due to the fact that there are opposing loci to which people are encouraged to direct their attention. Given these patterns of results, we suspect that people with greater-susceptibility genotypes are more likely to engage in culturally normative behaviors than are people without those genotypes. Thus, the association between genes and behavioral outcomes may be significant when there is an actively fostered set of behaviors within a cultural context, not merely when such cultural emphasis is absent.

So far these findings suggest that certain target genes increase or decrease susceptibility to specific aspects of the cultural environment. Although the empirical evidence is still quite limited, it appears that oxytocin-related genes may influence sensitivity toward social and emotional cues, and dopamine-related genes may influence sensitivity toward reward and punishment aspects of the environment. This specificity of genes, alone or together with other genes, in terms of their sensitivity to different aspects of environmental inputs, is a topic that will require further research, but at present, we can infer that these genes may not influence sensitivity to cultural norms in general.

Moreover, the relative frequencies of these genes vary within cultural groups (i.e., East Asians and European Americans): Some alleles that confer greater susceptibility (e.g., the G allele of *OXTR*) are more common among European Americans (Kim et al. 2010a, 2011), and other greater-susceptibility alleles (e.g., the S allele of *5-HTTLPR*) are more common among

East Asians (Chiao & Blizinsky 2010). Thus, there probably is not a single gene for cultural conformity per se. Rather, the complex genetic makeup of individuals predisposes them to be particularly sensitive to different aspects of the cultural environment in varied ways, and a person who is susceptible to emotional cues may not necessarily also be susceptible to reward and punishment cues (cf. Na et al. 2010). One should therefore be cautious about overgeneralizing the meaning of each specific gene-culture interaction.

We speculate that the interaction between genes and cultural meanings occurs in the brain. Although no gene-culture interaction studies have been conducted to look at neural activations, it is clearly assumed that neural processes are implicated, and the consideration of studies looking at neural correlates of culture-specific behaviors would suggest different models to consider.

NEURAL CORRELATES AND STRUCTURAL CHANGE

In this section, we present recent studies that used magnetic resonance imaging (MRI), functional MRI (fMRI), and EEG measures to examine structural change and neural correlates of culturally related psychological processes. This particular area within cultural neuroscience has been a subject of very active research, with studies on a wide range of topics that are largely consistent with behavioral and psychological findings and that illuminate the underlying neural mechanisms of these phenomena. Although our review of these studies is not meant to be comprehensive, we discuss some of the seminal corroborating studies in this area and, importantly, highlight studies that capitalize on the unique potential of neuroscientific measures to illuminate the psychological processes themselves.

Representations of Self Versus Others

Culture plays a crucial role in ascribing meaning and value to the self. Many cultural differences in psychology are based on the different ways that people across cultures construe the self. For cultures such as those in North America, the self tends to be seen as more independent, whereas for cultures such as those in East Asia, the self may be understood as more interdependent (Markus & Kitayama 1991). People from cultures that foster more independent self-construals tend to emphasize individual agency, uniqueness, and personal choice (e.g., Iyengar & Lepper 1999, Kim & Markus 1999 for national difference; Snibbe & Markus 2005, Stephens et al. 2007 for social class), while people from cultures that foster more interdependent self-construals tend to focus on maintaining harmony in relationships and fulfilling social obligations (Miller et al. 1990).

The self is also one of the most actively investigated topics in cultural neuroscience, and thus as a whole the topic presents a good collection of multiple methodological approaches, such as cross-national and cross-religious comparisons and priming of cultural concepts. Self-related neural activity in response to different situational and relational stimuli seems to parallel the findings from behavioral studies. For instance, one study found that both Chinese and Western participants showed greater activation in the medial prefrontal cortex (MPFC) when judging traits about the self versus familiar others (i.e., people well known but not close) (Zhu et al. 2007), consistent with past research on the MPFC in relation to self-judgments relative to other-judgments (Kelley et al. 2002, Lieberman et al. 2004). However, in this study only Chinese participants showed greater MPFC activation when thinking about their mother versus familiar others. Compared with British people, Chinese people also tended to show a weaker advantage for recognizing their own face versus familiar faces, as evidenced by reduced N2 amplitude in event-related potentials (ERP)—a response that has been linked to deeper processing of faces and the ability to differentiate them (Sui et al. 2009).

Aside from ethnic or national differences, religious differences may also be implicated in neural representations of self processes. Two studies found that people who hold Christian or Buddhist beliefs (versus the nonreligious) showed dampened patterns of neural activation in the ventral MPFC (VMPFC), which is associated with labeling stimuli as self-relevant (Northoff et al. 2006), when making self-referential judgments, perhaps because of a religious emphasis on denial of self (Han et al. 2008, 2010). Taken together, these findings appear to corroborate theoretical and empirical studies in cultural psychology that suggest that the conceptualization of self may be more or less overlapping with conceptualization of close others and may have a weaker or greater emphasis based on culturally construed meanings.

Some research has used cultural priming techniques together with neural measures to more effectively address questions surrounding the causal nature of cultural influence. In one study, Chinese participants primed with more independent (versus interdependent) self-construals showed greater activation of the right middle and inferior frontal cortex, which may be linked to self-recognition (Keenan et al. 2000), when viewing their own face compared with a familiar person's face (Sui & Han 2007). Another similar study examined the effect of self-construal priming on ERP responses to one's own face and a friend's face among British and Chinese participants. The results showed that culturally incongruent self-construal priming (i.e., independent self to Chinese and interdependent self to British) weakened the typical culture-specific pattern on the anterior N2 component (Sui et al. 2013). In a study with bicultural participants, priming Western cultural symbols led to increased neural differentiation of close others from the self in the VMPFC, while priming Chinese cultural symbols decreased differentiation (Ng et al. 2010). Other research has found that bicultural people primed with individualistic values exhibited greater MPFC activation to general trait descriptions of the self, whereas bicultural people primed with collectivistic values seemed to show greater MPFC activation to context-specific traits about the self (Chiao et al. 2009). Thus, neural indicators of stimuli discrimination may depend on the salience of cultural information, and similarly, the extent to which the same brain region is activated may vary according to salient cultural information and the way the self is construed in the broader culture.

Cognitive Processes

Cultural differences in cognition can be broadly organized according to two main systems of thought: analytic thinking, which tends to be more prevalent in North American and Western European cultures, and holistic thinking, which tends to be more prevalent in non-Western cultures (Nisbett et al. 2001). Whereas analytic thinking is generally characterized by greater attention to central objects, categorization according to formalized rules, and attributional tendencies that focus on dispositional causes, holistic thinking is characterized by greater attention to the field, categorization according to family resemblance or relational rules, and attributional tendencies based on situational causes (Nisbett et al. 2001).

Foundational research in the area of culture and cognition has been corroborated and extended using approaches from neuroscience. We describe a set of studies that we consider particularly influential because they illuminate ways in which the cognitive processes underlying certain behaviors may actually be different across cultures, even when the behavioral responses appear similar. We believe that these studies exemplify how neuroscientific technology may be used to investigate cultural psychological processes that are difficult to directly access otherwise.

In number processing, for instance, people from two different cultures may arrive at the same response when given the same numerical task, yet the psychological processes leading to that response may differ from each other. In a study by Tang and colleagues (2006), native Chinese and

English speakers engaged different brain regions when performing the same mental arithmetic tasks. There were no differences in the accuracy or reaction times of participants completing this task, yet patterns of brain activation revealed significant differences. In particular, whereas English speakers performing the addition task showed activation in language-related regions, such as the left perisylvian cortices (including the Broca and Wernicke areas), Chinese speakers showed stronger activation in vision- and space-processing regions, including visuo-premotor association areas. The authors of this research argue that these differences are likely shaped by language and other features of the cultural environment, such as education and learning strategies. These findings are consistent with previous research showing that talking aloud interferes with problem solving for Asian Americans, who may rely on language processes less during these tasks compared with European Americans (Kim 2002). The neural evidence on cultural differences in numeric processing, in conjunction with behavioral evidence on language use and problem solving, suggests rather convincingly that even the same response may be supported by quite different psychological processes, depending on culture.

Culture-specific patterns of brain activity are also found with attention-related tasks. East Asians exhibit greater activation in regions associated with attentional control or effort (e.g., frontal and parietal activation) when they are engaged in judgments that involve ignoring the context—a more effortful task in this culture—whereas European Americans show greater activation in the same regions when they are engaged in judgments that involve attending to the context (Hedden et al. 2008). These results show that the same brain regions are activated when people are engaged in culturally incongruent attentional tasks, regardless of the actual content of the task (i.e., ignoring the context versus attending to the context). In an ERP study, researchers demonstrated that East Asian Americans showed greater P3 amplitudes, which are thought to index attention to infrequent events, in response to contextually discrepant stimuli, compared with European Americans (Lewis et al. 2008). In a conceptually related study, more interdependent (versus independent) Japanese female participants who listened to words that did not match the spoken vocal tone (e.g., the word "satisfaction" spoken in a negative tone of voice) showed greater N400 ERP activation, which has been shown to indicate detection of semantic incongruity (Ishii et al. 2010).

East Asians and European Americans also seem to reconcile competing strategies for semantic judgments in categorization tasks via distinct brain regions (Gutchess et al. 2010). When they had to categorize stimuli based on a particular rule (i.e., relational or taxonomical) while ignoring the other conflicting rule, East Asians and European Americans performed at similar levels. However, their neural activations differed. East Asians in this study showed activation in frontal-parietal networks as they engaged in top-down controlled processes, whereas European Americans showed activation in the temporal lobes and the cingulate gyrus, indicating semantic information processing, top-down detection of conflict, and monitoring.

Evidence using neural measures also corroborates cultural differences in causal attribution. The processing of contextual information in certain brain regions, such as the left parietal cortex, may be sensitive to cultural information about causality (Han et al. 2011). In addition, European Americans tend to make inferences about a person's disposition more quickly and spontaneously than East Asians. Furthermore, European Americans show a stronger N400 response when judging incongruous versus congruous personal traits, whereas Asian Americans show no such response (Na & Kitayama 2011). A similar pattern of results was found in a study on spontaneous trait inferences among people from middle-class backgrounds (who tend to show more analytic cognitive styles) and people from working-class backgrounds (who tend to show more holistic cognitive styles; Grossmann & Varnum 2011, Kraus et al. 2010), such that middle-class participants exhibited greater N400 signaling to incongruous traits compared with working-class participants (Varnum et al. 2012). Across various neural measures, this research not only corroborates past behavioral research but also suggests that stimuli with particular meanings in one culture versus another may evoke distinct patterns of neural responses, depending on culture.

Emotions and Interpersonal and Group Processes

Culture moderates the process of emotion regulation as well as the way people feel in response to interpersonal and intergroup interactions. In line with past behavioral research demonstrating the cultural shaping of emotion regulation (Matsumoto et al. 2008, Tsai & Levenson 1997), several fMRI studies suggest that these cultural differences emerge at the level of neural activity. In one study, American participants were instructed to suppress emotion while viewing film clips eliciting disgust. Although participants reported experiencing reduced negative affect, they actually showed greater emotion-related responses in the right insula and the right amygdala (Goldin et al. 2008). The dissociation between self-report and brain activation in this study highlights one of the important advantages of neural measures—they can at times reveal responses that might have gone undetected otherwise, particularly for constructs such as emotion that have been somewhat difficult to capture in the past without self-report measures. Interestingly, a similar study conducted with Japanese participants did not find increased activation in the insula or amygdala during emotion suppression (Ohira et al. 2006). Although these studies do not directly compare different cultural groups, the divergent findings within each particular culture are informative for illustrating how similar investigations can yield different neural results, depending on the culture of the participants.

Individual and group interactions are influenced not only by one's own thoughts and emotions but also by what one perceives other people's thoughts or emotions to be. Theory of mind (ToM), or the ability to reason about beliefs, desires, and intentions, may be one mechanism through which people can very quickly and effortlessly make predictions about other people's mental states and then employ that information in social situations (Dennett 1987, Fodor 1987). Recent neural evidence has illuminated interesting differences in ToM processing across cultures. Children aged 8–11 years reading a ToM-relevant story or observing a ToM-relevant cartoon, for instance, showed VMPFC activation regardless of cultural background; but, monolingual American children showed greater activation in the right temporoparietal junction (TPJ), a region associated with mental state inference (Saxe & Kanwisher 2003), compared with bilingual Japanese children (Kobayashi et al. 2007). Similarly, research with American and Japanese adults demonstrated strong activation patterns for both groups in several regions that have been associated with ToM, including the right MPFC, right anterior cingulate cortex, and bilateral TPJ, yet monolingual Americans also showed greater activation in other ToM-related brain regions (e.g., bilateral temporal pole, right insula, and right MPFC) compared with bilingual Japanese (Kobayashi et al. 2006). These studies suggest that there may be some components of ToM that are processed similarly across cultures, whereas other components may be more culture-specific and are potentially underpinned by different neural processes, depending on culture. However, the psychological meaning of these differences is not yet clear.

A related study on the ToM-related experience of empathy—vicariously feeling what another person feels—found that, although both European American and Korean participants showed greater activation in the left TPJ when observing the emotional pain of an in-group versus an out-group member, this effect was stronger for Koreans than European Americans (Cheon et al. 2011). Additionally, research examining the experience of empathy in response to anger expressions showed that Chinese participants instructed to empathize with a person with an angry face showed greater activation in the left dorsolateral prefrontal cortex, a region associated with emotion regulation, whereas German participants showed stronger responses in the right TPJ, right inferior and superior temporal gyri, and left middle insula—regions typically involved in empathy and emotion processing (de Greck et al. 2012). This study is particularly interesting given that it demonstrates that the same information may be processed through different neural paths in different cultures, perhaps leading to different psychological responses. Taking together these studies on ToM and empathy, it seems possible that ToM ability and empathy are underpinned by a variety of psychological processes, as reflected by different patterns of neural activation. Importantly, the degree of neural response to ToM- or empathy-related tasks seemed to vary according to cultural background. These divergences in neural activation raise the possibility that the psychological and neural pathways for social connections with others differ across cultures.

In every culture, social hierarchies are important, yet the way people navigate these social structures can vary depending on the normative values and behaviors within a particular culture. An fMRI study on culture and dominance versus subordination nicely illustrates this point. Participants in this study were shown the outlines of dominant and subordinate body displays, and results showed that American and Japanese participants had selective neural activation in the caudate nucleus and MPFC in response to body displays that were more reinforced in their respective cultures. That is, Americans produced this pattern of activation when viewing dominant displays, whereas Japanese produced the same pattern of activation when viewing subordinate displays (Freeman et al. 2009). The authors suggest that parts of the MPFC may be implicated in retrieval or representation of self-relevant cultural behaviors, such as dominance or subordination, while the caudate may link those behaviors to a culture-bound reward value. By demonstrating that people from different cultures may at times show the same pattern of activation in response to quite different sets of stimuli, this study illustrates the importance of incorporating cultural meanings in neuroscience.

Taken together, these studies demonstrate that the ways culture affects neural responses to social information and stimuli present a fairly complex picture. Sometimes a similar pattern of neural activation may occur in response to different stimuli across cultures, depending on the cultural meaning of the stimulus (e.g., effortful attention; Hedden et al. 2008). Yet at other times, different patterns of neural activation can underlie seemingly similar behavioral outcomes because people from different cultures may produce the same behavior through different psychological processes (e.g., arithmetic task; Tang et al. 2006). We believe that these research areas are likely to lead to greater theoretical advancements and thus warrant future investigation.

Neuroanatomical Differences

Although most studies in cultural neuroscience thus far have examined brain activity using fMRI or EEG measures, some have used structural MRI to address the question of whether neuroanatomical differences reflect cultural influences. In particular, might engagement in different cultural contexts be associated with systematically different brain structures? In fact, some studies suggest that this is the case. For instance, there are anatomical differences in the middle left frontal gyrus, the inferior middle left temporal gyrus, and the superior parietal left lobule of English-speaking Caucasians versus Chinese-speaking Asians (Kochunov et al. 2003) and hemispheric-shape differences between Europeans and Japanese (i.e., hemispheres are relatively shorter and wider for Japanese compared with Europeans; Zilles et al. 2001). Other research shows that Americans not of Asian descent differed from Chinese Singaporeans in the cortical thickness of bilateral frontal, parietal, and medial-temporal polymodal association cortices (Chee et al. 2011), and the authors speculate that one potential explanation for these results is that these structural differences are linked to the use of different cognitive strategies, such as holistic versus analytic thinking. These neuroanatomical differences between cultural groups potentially provide evidence for neural plasticity. Yet, although culture and language are among the possible explanations for the structural differences found in these studies, these cross-ethnic comparisons raise several other potential explanations, including environmental and genetic factors.

One way to isolate the impact of language learning in particular may be to examine the case of second-language acquisition. There is evidence, for instance, of differences in gray matter density between English monolingual subjects and Italian-English bilingual subjects in parietal cortex regions indexing meaning-sound associations (Mechelli et al. 2004). Another study found that Europeans who did not speak Chinese showed differences in gray and white matter density compared with Chinese speakers, and this difference held whether the Chinese speakers were native Chinese monolingual subjects or Europeans who were bilingual in English and Chinese (Crinion et al. 2009; see Green et al. 2007 for a review of linguistic effects on brain structures). Given that language systems may be highly sensitive to culture-specific input, the comparison of different language speakers from similar ethnic or national backgrounds seems to be a particularly effective, systematic way to address the issue of neuroplasticity.

PHYSIOLOGICAL PROCESSES

In this section, we focus on cultural differences in cardiovascular, neuroendocrine, and immune responses, which result from underlying neural processes. Studies in cultural psychology show that there are culturally shared, distinct meaning systems that can lead to divergent outcomes in psychological processes and social behaviors. Central elements of these meaning systems include values, which affect people's sense of good and bad, and norms, which affect people's sense of expectations within the social environment. Thus, one consequence of facing cultural meaning violation through engaging in actions that are discordant with cultural values and expectations may be psychological distress (Heine et al. 2006, Proulx & Heine 2008). In many studies examining physiological functions, the key psychological factors of interest are distress and threats induced by psychological and social causes (Blascovich & Tomaka 1996, Dickerson & Kemeny 2004), and thus experiencing cultural meaning violation could lead to detectable changes in biological functioning. In the following section, we review findings demonstrating how one's subjective psychological state may affect biological states, and how biological functioning may be implicated in cultural processes.

Social Relationships

One line of research examining how people from different cultures vary in their biological responses to a given situation focuses on the effect of social support use (see Sherman et al. 2009 for a review). Compared with European Americans, Asians/Asian Americans are less willing to seek explicit social support and instead rely more on implicit social support—spending time with or thinking about close others without talking about one's stressor—because they are more concerned about potentially disturbing their social network (Kim et al. 2008, Taylor et al. 2004). Thus, explicitly asking for social support may be a source of distress among Asians/Asian Americans. Taylor et al. (2007) investigated psychological and biological outcomes of seeking explicit and implicit social support. Asian/Asian American and European American participants underwent a lab stressor (Kirschbaum et al. 1993) and were randomly assigned to either an explicit social support condition (i.e., writing a letter asking for advice and support about the stressor from a close other) or an implicit social support condition (i.e., writing about the aspects of a close group that is important to them). The study included both psychological and biological (i.e., salivary cortisol) measures of stress experiences. The results showed that according to both measures, engaging in the culturally discordant form of social support seeking for either cultural group increased stress levels.

Similarly, perceiving that one is lacking a social network from which he or she may draw support has different biological consequences in different cultures. One implication from research on culture and social support seeking is that people from East Asian cultural contexts may not equate positive social relationships with their availability for social support, and consequently they may not experience a great deal of stress if they perceive that their social network provides lower levels of explicit social support. For instance, one study (Chiang et al. 2013) examined the link between proinflammatory cytokines and perception of support availability among Asian Americans and European Americans. Proinflammatory cytokines are part of an innate immune response that is adaptive in the short term but can have long-term negative impacts such as elevated chronic inflammation, which has been implicated in many chronic diseases (Ridker et al. 2000). Specifically looking at the proinflammatory cytokine interleukin-6 (IL-6), this study found that culture was a significant moderator of the link between perceived support availability and the level of IL-6. 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 statistically significant.

Thus, a "culturally mismatched" environment—having to engage in cultural contexts that differ from what one is familiar with—can be a cause of distress. Taking a more experimental approach, one study examining social class as a cultural context found that first-generation college students, who tend to have stronger interdependent relational norms, showed a stronger cortisol response to a lab stressor when the college culture was described as independence focused (i.e., emphasizing personal self-expression and intellectual journey) than when it was described as interdependence focused (i.e., emphasizing community and social connections) (Stephens et al. 2012).

Cognitive and Emotional Processes

Cultural differences in the biological effects of situational factors are also found in relation to cognitive and emotional processes. East Asians and European Americans who are from cultural contexts with divergent views on the value of verbal expression (Kim & Sherman 2007) differ in how they are affected by verbal expression of thoughts as indicated by their cortisol response. Speaking thoughts aloud decreases cortisol responses to a challenging cognitive task among European Americans, who are from a cultural context that considers verbal expression to be beneficial for thinking, whereas the same action bears no such benefit among East Asian Americans, who are from a cultural context that does not share the value of verbal expression (Kim 2008). Relatedly, these general patterns of cultural differences in the impact of expression extend to emotional expression as well. Butler and colleagues (2009) found that European Americans who suppressed their emotions while watching film clips meant to elicit negative emotions had significantly higher blood pressure than those given instruction allowing expression of their negative emotions, but Asian Americans who suppressed their emotions had marginally lower blood pressure than those who expressed their emotions. These studies demonstrate that cultural expectations and meanings regarding social interactions, specifically how to appropriately engage in social support use, express thoughts, and regulate emotion, lead to culture-specific biological consequences of these actions.

Looking at regional differences between American southern and northern males in their response to insults, Cohen et al. (1996) measured both cortisol and testosterone, a hormone associated with aggression and dominance, and found that southern males, who see insults as a threat to their honor, showed marked increases in cortisol and testosterone when insulted. However, northern males, who are not as concerned about the notion of honor, did not show such responses (Cohen et al. 1996).

Religion also moderates how people physiologically respond to environmental stimuli. Weisbuch-Remington et al. (2005) examined cardiovascular responses to subliminally presented Christian religious symbols that were negative (e.g., image of a demon) or positive (e.g., image of Christ) among Christians and non-Christians. Using the biopsychosocial model of challenge and threat (Blascovich & Tomaka 1996), this study found that religious affiliation moderated how participants' cardiovascular state was affected by the religious symbols. Christians responded to negative images with more threatened cardiovascular reactions compared with their reactions to positive images, whereas non-Christians did not show such a difference.

Taken together, these studies illustrate that experiences in shared sociocultural contexts, such as national, regional, social class, and religious contexts, give rise to the psychological meaning of situations, actions, and objects and thus moderate the relationship between stimuli and psychological and biological outcomes. The reviewed studies show that these biological functions mostly corroborate behavioral findings in that culture moderates the relationships between stimuli and outcomes in consistent and predicted manners. Use of physiological measures could reduce certain methodological concerns common in self-report. Moreover, as physiological functions are associated with numerous health outcomes, such as inflammation or cardiovascular disorders, these investigations may point to important consequences of culture-specific processes.

Neurotransmitters and Social Behaviors

Although the use of biological responses as outcome variables is more common, a small number of studies investigate more mechanistic roles of biological measures in sociocultural processes. Oxytocin, a peptide produced in the hypothalamus that functions as both neurotransmitter and hormone (Hatton 1990), has been the focus of much investigation. An array of prosocial tendencies, such as social bonds, trust, cooperation, affiliation, and positive communication, have been associated with oxytocin, examined as both plasma oxytocin (Feldman et al. 2007) and exogenously administered oxytocin (Ditzen et al. 2009, Kosfeld et al. 2005) in animals and humans (see Meyer-Lindenberg et al. 2011 for a review). Yet recent research suggests that rather than simply promoting prosociality, oxytocin may increase sensitivity to important social cues. For example, in humans oxytocin increases the ability to accurately attribute the emotions and mental states of others (Bartz et al. 2010, Domes et al. 2007), and in rodents it increases the ability to accurately detect disease-infected others (using oxytocin-gene-knockout rodents, Kavaliers et al. 2004; see Kavaliers & Choleris 2011 for a review). Moreover, another study shows that oxytocin may increase in-group bias among humans (De Dreu et al. 2011). Using the experimental method of administering intranasal oxytocin spray, this study found that oxytocin increased the degree to which participants favored in-group others and derogated out-group others (see Bartz et al. 2011, Meyer-Lindenberg et al. 2011, Miller 2013 for relevant reviews).

These psychological tendencies and behaviors associated with oxytocin—empathic accuracy, accuracy in pathogen detection with others, and ethnocentrism—are crucial elements in the maintenance of sociocultural processes. For instance, empathic accuracy may be a necessary ability to gauge others' reactions and approval/disapproval of one's actions. Sociocultural norms and valuations are often reinforced and maintained through social interactions (Fiske et al. 1998, Na et al. 2013), and thus one's ability to perceive others' intentions may be a crucial psychological mechanism for the maintenance of cultural systems (Kim et al. 2011).

Ethnocentrism, in which people favor familiar in-group others over unfamiliar out-group others, is a basic part of human sociality. This tendency may first be implicated in sociocultural processes in that psychological closed-ness in ethnocentrism would serve to maintain and strengthen culture-specific behaviors. Moreover, it may play a role in shaping certain aspects of cultural diversity. It has been argued that ethnocentric patterns of social behaviors, which are more common in certain cultures than in others, may serve as a pathogen-avoidance mechanism (Fincher et al. 2008, Kavaliers & Choleris 2011, Schaller & Murray 2008). Regions with higher pathogen prevalence tend to develop collectivistic cultures that foster stronger in-group biases than do regions with lower pathogen prevalence (Fincher et al. 2008). Thus, oxytocin, which seems to be causally involved in these social processes, may play an important role in the emergence and maintenance of sociocultural systems. There are likely other neurotransmitters and hormones that are associated with various social behaviors. The case of oxytocin provides one example of how neurotransmitters may have important functions in these larger collective processes and also an example of how the study of mind and culture can incorporate biological processes beyond simply looking at them as outcome measures. This is a particularly exciting and important issue raised by taking the theoretical perspective of the interplay between culture and biology.

INTEGRATION AND FUTURE DIRECTIONS OF CULTURAL NEUROSCIENCE

The studies reviewed herein demonstrate that cultural influences are engaged at many different levels of biological functions. These studies also provide more complete information on the mechanisms of cultural influence, as neural evidence provides researchers with a more precise understanding of how meanings shaped and shared by cultural experiences trigger a neural, psychological, and behavioral chain of events, and of how these events are coordinated and maintained within a person. From a neuroscientific perspective, the study of culture provides valuable information on the ways in which certain neural structures may serve similar functions across cultures while at the same time being malleable in response to cultural inputs.

Following our review of the current state of cultural neuroscience research, we conclude with future directions. In a way, these involve current methodological issues that have limited a causal understanding of the interplay of two main constituent factors: culture and genes. Both are factors that are difficult to study in a true experiment, at least among humans, and thus the field has inherent uncertainty about the causal roles of these factors. Our recommendation is to borrow from the methodological innovations of cultural psychology and cultural neuroscience to increase confidence in the causal role of cultural and biological factors.

First, most of the studies to date with perspectives from cultural neuroscience use cross-sectional designs comparing genetic associations, neural correlates, and physiological responses among different cultural groups. In our view, one of the chief theoretical gains of cultural neuroscience is the demonstration of adaptability and its resultant diversity in biological functioning, along with greater appreciation for the role of biology in psychological and behavioral processes. Although these studies clearly demonstrate cultural diversity in neural functions, they do not necessarily show the process through which cultural factors influence them, and the causal role of cultural experiences is therefore unclear. Thus, we propose that there should be greater empirical efforts in cultural neuroscience research to investigate the psychological consequences of cultural change.

One of the most direct and convincing ways to understand the impact of cultural contexts is to look at change in cultural environments and subsequent changes in behavior. As the cultural contexts in which people are engaged or the meanings construed in cultural contexts change, so too should the way people process information, experience emotion (De Leersnyder et al. 2011), and interact with others (Taylor et al. 2004). Moreover, culture-specific psychological processes are quite responsive to situational cues, such as cultural icons (Hong et al. 2000), relational concepts

(Kühnen et al. 2001), and language (Ji et al. 2004, see Oyserman & Lee 2008 for a review). Borrowing from these methods, research in cultural neuroscience may focus on people who undergo cultural changes via acculturation (Kim et al. 2010b), or situational malleability, using methods such as experimental priming (Ng et al. 2010, Sasaki et al. 2013). Investigations of both immediate situational shifts as well as slower developmental or stable and long-term changes will complement each other and provide insight into biological malleability.

A second question is how to piece together the findings from different areas within cultural neuroscience into an integrative framework. Integration is required at many levels of analysis. As suggested by Li (2003), there is evidence of cultural influence on cognitive and developmental plasticity at multiple levels, from the more macro level of biological evolution to the more micro levels of neural and genetic change. We posit that a major challenge for researchers now is to demonstrate how changes at one level can lead to changes at another. For example, for greater understanding of the gene-culture interaction model, more research must examine the neural and molecular mechanisms linking cultural and genetic factors to culture-specific behavioral outcomes. Studies investigating gene-environment interactions can inform the mechanisms of the gene-culture interaction model. Studies have shown how environmental input triggers changes in gene expression (Cole et al. 2007) and implicates physiological responses (Rodrigues et al. 2009) and brain reactivity (Pezawas et al. 2005) that may explain psychological and biological outcomes. A similar systematic and mechanistic approach is needed to investigate the influences of culture and genes. In so doing, investigators may attend to the entire chain of neural, physiological, psychological, and behavioral events to gain a more precise understanding of which parts of the chain are affected by culture and genes.

Third, more research should use process-oriented approaches within neural and genetic levels of investigation, as well as between these levels, as suggested above. For instance, it is important to investigate how culture influences processes involving multiple genes or the functional connection of different neural networks. There are novel theoretical perspectives and methodological tools available to address some of these questions, such as pathway analysis in genetics (Zhong et al. 2010) and neural network analysis (Bullmore & Bassett 2010, Butts 2009). These available models will be of great value to further advance understandings of neural processes and pathways that underlie human behaviors and psychological outcomes.

Furthermore, it is important to note that genetic-association studies are ultimately correlational and that the causal role of any given gene is therefore still an open question. One way to address this issue may be through the use of experimental manipulation of exogenous hormones. For instance, as mentioned earlier, studies with intranasal oxytocin administration show that oxytocin can be safely used in experimental settings (MacDonald et al. 2011) and that the administration may increase the salience of social cues (Bartz et al. 2011). Given this evidence, the use of experimentally administered exogenous hormones may be a particularly good way to directly test the mechanistic role of target neurotransmitters. Similar experimental manipulation is possible for serotonin using acute tryptophan depletion, increasing the potential for more causal models. Although these medical drugs should be administered with caution, at least theoretically, such experiments may be useful.

Finally, we consider the most central necessity of the field to be the development of new theories that are specific to cultural neuroscience. Up to this point, most studies have been based on existing theories from behavioral studies in cultural psychology, finding empirical evidence with neural correlates and physiological responses that parallel behavioral and self-report responses. Although this approach has been and is useful for the reasons articulated earlier, there is also a great need for novel theoretical frameworks that will allow researchers to take advantage of the unique potential of neuroscientific methods and generate new research questions.

These possibilities are reminders of the fact that cultural neuroscience is young and thus poses many questions that have yet to be answered. However, its youth also highlights its unique potential in addressing the age-old question of nature and nurture as joint determinants of human behaviors and the question of how these influences come about. Whether through behavioral or neural studies, the field of cultural neuroscience underscores the importance of meaning making as a key factor in psychological and biological processes.

SUMMARY POINTS

1. Cultural neuroscience is a unique combination of perspectives that investigates how culture has implications not only for shared environments, as has historically been shown in cultural psychology, but also for the brain, physiology, and genes, which have generally been within the purview of neuroscience.
2. Genes and culture mutually influence each other and influence psychological tendencies at the macro level, via gene-culture coevolution, and at the micro level, in gene-culture interactions. The same genetic tendency can be manifested differently depending on the cultural context.
3. Theoretical advancement is especially evident from studies demonstrating divergent patterns of neural activation that underlie seemingly similar behavioral outcomes.
4. Violation of cultural meaning can affect cardiovascular and neuroendocrine responses, and this has implications for health and well-being.
5. Cultural neuroscience provides cultural psychology with information about the genetic factors interacting with culture, neural mechanisms underlying cultural differences, and physiological responses linked to psychological processes.
6. Cultural neuroscience provides neuroscience with information about how cultural inputs have implications for malleability in genetic expression, neural structure and activity, and physiological responses linked to psychological processes.
7. More cultural neuroscience research should examine cultural change and the resulting psychological consequences with a process-oriented and experiment-based approach.
8. New theories and integration of genetic, physiological, and neural evidence are required for cultural neuroscience to move toward a more holistic understanding of the mind.

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