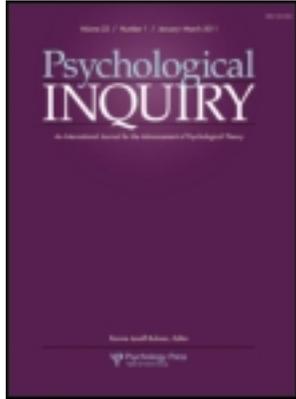


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### Constraints, Catalysts and Coevolution in Cultural Neuroscience: Reply to Commentaries

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## REPLY

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### **Constraints, Catalysts and Coevolution in Cultural Neuroscience: Reply to Commentaries**

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#### **Introduction**

In 1906, Ramon y Cajal described the brain as “a world consisting of a number of unexplored continents and great stretches of unknown territory” (Santiago, 1920). Nearly a century later, human neuroscience researchers have sought to map the structural and functional features of the brain, much as Magellan in 1520 circumnavigated the globe discovering for the first time great stretches of ocean and land that compose our physical world. Yet many opportunities and challenges in cultural neuroscience make much of this contemporary scientific journey ongoing and perpetual. For instance, scientific models depend on identifying and discovering evidence for causal mechanisms—such as how genetic and experiential factors constrain and evoke neural development within and across generations; yet the technology or access to technology for testing causal mechanisms in gene, brain, or behavior remains limited. Novel biological theories such as culture-gene coevolutionary theory provide a fresh lens for contemporary psychologists and neuroscientists to view the human mind and brain as a by-product not only of gene–environment interactions but also of human culture.

What is human culture? The notion of human diversity has compelled intellectual inquiry for centuries and at the nexus of anthropology and psychology, scholars agree that at minimum, culture refers the sets of values, practices, and beliefs that define groups and people within and across geography. Culture is both created and transmitted by human behavior; as such culture–gene coevolutionary theory argues that cultural traits, like genetic traits, can be selected on by evolutionary forces. Furthermore, when culture is created, this niche construction can alter environmental factors or pressures that interact with genetic mechanisms in the production of psychological and biological

processes that give rise to human behavior. In broadest stroke, the study of culture has progressed in leaps and bounds in ways that enable us to better understand how to conceptualize and study the how and why of human nature.

In our target article, we presented from a historical perspective conceptual developments that led to the emergence of cultural neuroscience as a field, and articulated a framework for examining cultural and biological interactions of human behavior. We then presented empirical advances in how culture affects neural mechanisms of cognitive, affective, and social processes as well as the role that culture–gene interactions across evolutionary, developmental, and situational timescales play in shaping mental and neural architecture. As the field of cultural neuroscience is still in its infancy, there are key constraints on our existing knowledge and empirical approaches to how cultural influences on the human brain are studied, and the commentaries to our target article are testament that scientific ingenuity and conscientiousness will simultaneously guide us toward better understanding the legacy of cultural and genetic inheritance on mind, brain, and behavior.

#### **Broadening the Toolbox: Methodological Constraints in Cultural Neuroscience**

*The expectations of life depend upon diligence; the mechanic that would perfect his [or her] work must first sharpen his [or her] tools.—Confucius*

Cultural neuroscience seeks to examine the mutual influences of culture and mind across multiple levels of analysis (e.g., behavior, genes, the brain, physiological processes, cultural norms and practices); numerous

existing theories of how cultural and biological mechanisms give rise to mind and behavior abound. However, existing methodological constraints in cultural neuroscience hamper attempts to distinguish and sort these theories from one another. Here we elaborate on key constraints introduced by commentators and address, when possible, ways of overcoming these constraints.

One of the main methodological and theoretical issues brought up in these commentaries is whether differences in brain activation between cultural groups reflect differences in cultural processes (Han, this issue; Immordino-Yang, this issue). The “transcultural neuroimaging” approach is critical in cultural neuroscience, not only because it is the most commonly employed method in the cultural neuroscience literature (see some examples listed in Han, this issue), but also because neuroimaging is capable of detecting cultural variations in neural processes in the absence of significant behavioral differences (as mentioned in our target paper and in Immordino-Yang, this issue; Chiao, 2010). In other words, when interpretation of the data has to rely only on neural results, one may only be able to give post hoc explanations, which is the common problem of reverse inference in cognitive neuroscience (Poldrack, 2006, 2008). Such concerns may be mitigated by conducting follow-up studies to indeed test whether the presumed psychological processes associated with neural activity may indeed predict the cultural differences of interest.

Yet cultural variations in patterns of neural responses in the absence of associated behavioral processes may in itself be a meaningful cultural phenomenon worthy of investigation rather than an unintended inconvenience. The influence of culture may not be homogenous on cognition and behavior, because cognition and behavior are not always under the same constraints (e.g., maintaining counternormative cognitions and attitudes but not engaging in counternormative behavior). Similarly, Norenzayan and Heine (2005) distinguished different levels in which psychological attributes may vary in regards to universality. For instance, *existential universals* refer to cognitive processes or tools that are available across cultures, yet may have different functions or levels of accessibility across cultures (see Norenzayan & Heine, 2005).

Dissociations in the observation of differences in behavior and neural activity between cultural groups may be especially likely in studies involving existential universals. One mechanism for this dissociation may be participants from two separate cultural groups relying on different underlying cognitive tools and processes to solve the same type of problem, manifesting a cultural difference in psychological means or strategies employed, but a cultural convergence on the solution or behavioral outcome. Consistent with this notion, a study by Tang and colleagues (2006) revealed that Chinese and English-speaking participants exhib-

ited different patterns of neural activity when solving basic arithmetic problems (e.g.,  $3 + 6$ ) and number comparisons. Although Chinese-speaking participants exhibited greater activity in regions involved in visual-spatial and premotor processing during simple numerical tasks, English-speaking participants exhibited greater activity in regions involved in verbal processing, such as the perisylvian cortices. In sum, such findings in transcultural neuroimaging studies suggest that the absence of behavioral differences in the presence of differences in neural responses should not necessarily be unexpected, and may itself be reflecting a culturally relevant phenomena.

The absence of behavioral differences in the presence of differences in patterns of neural responses may also be partly due to differences in sensitivity between measures from two levels of analyses (i.e., behavioral vs. neural; Chiao et al., 2010) and the practical aspects of using expensive cognitive neuroscience equipment (Park, this issue). Typically, the sample sizes are higher in social or cross-cultural psychological experiments than in cognitive neuroscience experiments due to differences in effect sizes related to studying distal and proximate effects of psychological and neural processes on behavior (Chiao et al., 2010). Hence to achieve the same statistical power to detect behavioral differences in cultural neuroscience, one should increase the number of subjects to a level similar to that in social psychological experiments, which practically may not be feasible. Nonetheless, we argue that, under some circumstances, neural data from transcultural neuroimaging techniques may be sufficiently conclusive, and hence are able to index cultural influence to the brain. For instance, as alluded to by Meyer, Way, and Eisenberger (this issue), across two studies we have shown differential responses within empathic-related areas, temporoparietal junction (TPJ) and medial prefrontal cortex, preferentially elicited by Koreans and Caucasian Americans, respectively, even when the same empathy task was used (Cheon et al., 2011; Mathur, Harada, Lipke, & Chiao, 2010). This pattern of results may reflect the difference in predominant empathic strategies across cultures: TPJ for a rule-based, third-person perspective strategy among Koreans and medial prefrontal cortex for a stimulating, first-person perspective strategy among Caucasian Americans.

We nevertheless agree that similar to cognitive and social neuroscience, cultural neuroscience also shares the potential for reverse-inferences (Poldrack, 2006). Effective solutions to methodologically improve the transcultural neuroimaging technique were suggested in the commentaries. Han (this issue), for instance, recommended the use of a cultural construct as a mediator of participant group and group differences in neural activity, which reveals potential cultural mechanisms underlying differences in neural activity. For example, Ma and colleagues (2012) recently showed that group

differences (e.g., Danes vs. Chinese) in TPJ activity were mediated by a cultural value of self-construal (Singelis, 1994). This mediation approach was previously used in other papers involving different cultural values and methodologies. Similarly, with a different methodology, Na and Kitayama (2011) showed that cultural group difference (e.g., Asian and European Americans) in spontaneous trait inference reflected in N400 Event-related potential component was also mediated by self-construal (Singelis, 1994).

An alternative mediation model is possible whereby brain activity, rather than cultural norms, may serve as a mediator between cultural values and behavior in a given task. For instance, the relationship between cultural differences in hierarchy preferences, as indexed by social dominance orientation (Pratto, Sidanius, Stallworth, & Malle, 1994), and ingroup biases in empathy ratings was found to be partially mediated by preferential activity in the left TPJ toward the suffering of ingroup relative to outgroup members (Cheon et al., 2011). Both mediation models provide additional clarity regarding the role of cultural values in the effect of culture on neural mechanism and on behavior.

Nonetheless, using a cultural construct from a self-report measure as a mediator posts some problems. First, as mentioned in Ng, Morris, and Oishi (this issue), there are some inherent problems of using self-report variables in cultural comparison studies. The *deprivation-based preference* problem, for instance, arises when respondents report what they unrealistically desire to be, as opposed to their actual selves (Peng, Nisbett, & Wong, 1997). In addition, the *reference-group effect* refers to when people judge themselves in comparison to others in their own culture and ignore people from other cultural groups (Heine, Lehman, Peng, & Greenholtz, 2002). Another potential drawback of the use of mediation as a statistical technique is that it may not give conclusive proof for causation; instead causation itself is an assumption in a model (Judd & Kenny, 2010). Because, as Ng et al. (this issue) argue, one advantage of cultural neuroscience is to avoid heavy reliance on the use of self-report in cross-cultural comparison research, the use of self-report cultural constructs through the mediation approach in transcultural neuroimaging should also be conducted with caution.

One promising alternative for future transcultural neuroimaging studies may be to use cultural tasks reflecting "culturally prescribed means to achieve cultural mandates" (Kitayama et al., 2009), instead of relying solely on self-report questionnaires of cultural values as potential mediators or moderators of the relationship between neural activity and behavior. An advantage of cultural tasks for transcultural neuroimaging is that they can either be administered outside of the MR scanner, or could be integrated into the scanning runs to identify whether patterns of neural activity on

the cultural task correspond to or predict patterns of activity on the behavioral outcome of interest being compared across cultural groups.

From the commentaries, it is quite clear that current cultural neuroscience research relies too substantially on correlational data (Han, this issue; Meyer et al., this issue; Sasaki, this issue). This is essentially true for neuroimaging studies when cultural groups are often defined by cultural origin, such as country, geography and socioeconomic status (Freeman, this issue; Gutchess & Goh, this issue; Han, this issue), hence inevitably creating a quasi experimental design in nature. One suggested solution (Han, this issue) is to employ a situated cognition approach (Oyserman & Lee, 2008; Oyserman, Sorensen, Reber, & Chen, 2009) by investigating how "priming" culture influences the brain. Recent studies reveal the viability of cultural priming methods for neuroimaging studies and elucidate the neural mechanisms underlying cultural priming and its effects. For instance, areas in the midline structures of the brain (e.g., the middle frontal cortex, ventral medial prefrontal cortex, and dorsal medial prefrontal cortex) were shown to be involved in processes of cultural priming of individualism and collectivism (Harada, Li, & Chiao, 2010; Ng, Han, Mao, & Lai, 2010; Sui & Han, 2007). Sasaki (this issue) also demonstrates the utility of priming for testing the dynamic relationship between genes and the activation of religion-relevant knowledge on prosociality (Sasaki et al., in press).

The cultural priming method in cultural neuroscience may also be susceptible to some challenges. For instance, how specific are cultural priming effects? Priming power, as opposed to priming culture, was found to influence analytic and holistic processes (Smith & Trope, 2006), which are components of the cognitive system that is thought to underlie some Eastern/Western cultural differences in cognition and behavior (Nisbett, Peng, Choi, & Norenzayan, 2001). Consequently, priming methodology suffers from a "many-to-one" issue, but it may also be affected by a "one-to-many" problem, such that priming culture activates other neural and cognitive processes that are not necessarily culturally related. Because these may undermine the causality argument of applying priming methods to cultural neuroscience, future research is needed to develop greater specificity and a better understanding of the consequences of the cultural priming phenomena. Equally important, we still do not know for certain whether cultural priming effects resemble the dynamical processes of cultural influences in the real world (for compelling arguments on dynamic processes in culture, see Christopoulos & Hong, this issue; Meyer et al., this issue).

Many suggestions were given in the commentaries for cultural neuroscientists to better understand neural mechanisms underlying cultural processes as they happen in the real world (Christopoulos & Hong, this issue;

Immordino-Yang, this issue; Park, this issue). For instance, studying the neural processes of acculturation and biculturalism would shed light on the real-world dynamical processes in acculturation (Christopoulos & Hong, this issue; Park, this issue), hence improving ecological validity to the theories and findings in the field. We agree with Park (this issue) that most research in cultural neuroscience has been disproportionately focused on bicultural individuals who were moved from non-Western countries to Western countries (e.g., Chiao et al., 2010; Harada et al., 2010). It would be informative to see the differences in the brain processes between bicultural individuals who transferred *from* non-Western countries and those who transferred *to* non-Western countries. Such research will also allow us to answer the boarder question on the relationship between culture and neuroplasticity (Christopoulos & Hong, this issue; Freeman, this issue; Park, this issue). That is, how much (or how little) culture can shape the brain functionally and/or anatomically (Park, this issue) given the constraint of plasticity in the brain (Freeman, this issue). Indeed, being able to answer such questions would have important implications due to the rapid globalization process (Christopoulos & Hong, this issue).

Another promising insight proposed in the commentaries that may help to strengthen the causality and ecological validity of cultural neuroscience is employing the anthropological approach (Immordino-Yang, this issue; Roepstorff, this issue). This approach emphasizes elucidating “how emergent dynamics may happen in interaction between concrete individuals” (Roepstorff, this issue, p. 61). Immordino-Yang (this issue) gives an elegant example from her research using ethnographic approaches with neuroimaging methodology to demonstrate the differences between Chinese and American participants in neural processing of awareness and assessment of their feelings. Strikingly, cultural difference in this study emerges as neutral description. Hence, complementing such methods with a cultural-manipulation paradigm such as priming would be promising in cultural neuroscience.

As with anthropology, cultural neuroscience will also benefit from integrating perspectives from sociology (Ng et al., this issue), especially with regards to generalizability of the theories and findings. We agree that socioecological factors that are objectively presented in the environment, such as socioeconomic status, residential mobility, unemployment, climate, and urban living (Meyer et al., this issue; Oishi & Graham, 2010), have not yet received much attention in cultural neuroscience. This is despite the fact that such factors have been found to influence cognition in a similar way to more traditional definitions of cultural group. For instance, working-class Americans were found to make decisions similar to what would be expected from collectivists (Stephens, Fryberg, & Markus, 2011;

Stephens, Markus, & Townsend, 2007). We envision that neuroscience would bridge cultural psychology with sociology such that we may gain insight as to how social ecological factors influence cultural behaviors.

### Cause as Catalyst: Understanding The Mechanisms of Cultural and Biological Change

*Shallow men [and women] believe in luck or circumstance. Strong men [and women] believe in cause and effect.*—Ralph Waldo Emerson

When incorporating cultural and neural measures to understand how the mind and brain work, a key aspect to keep in mind is that both cultural and biological processes operate dynamically, but at different rates of change that can both ease and complicate attempts to discern causality across dual processes. Due to the fact that genetic selection is much slower than cultural selection (Richerson & Boyd, 2005), skepticism regarding the timescale and causality between these factors arises (Meyer et al., this issue; Ng et al., this issue; Park, this issue; Sasaki, this issue). Here, we integrate some of these concerns and suggest future directions to supplement the extant, correlational research on culture–gene coevolutionary theory. We hope to broaden the scope of gene–culture interplay that has influenced both evolutionary and modern behavior through describing how a “source analysis” approach can help inform the “cultural mapping” approach and vice versa.

Although Ambady and Bharucha (2009) cautioned against the source analysis approach (as mentioned by Freeman, this issue), we posit that understanding how immense variability emerged across the world due to ecological pressures is a worthwhile endeavor, if approached systematically. Thus far, the research following this source analysis approach is still in the nascent stage of cross-national correlations. Much of the culture–gene coevolutionary research thus far (Chiao & Blizinsky, 2010; Mrazek et al., 2013) relies on an explanatory variable of environmental pressure, such as pathogen prevalence, population density, food deprivation, vulnerability to natural disasters, or historical conflict (Fincher et al., 2008; Gelfand et al., 2011). Ng et al. (this issue) aptly note that a major limitation of this kind of theorization is that some of these ecological variables may be too recent of a phenomenon to have influenced genetic selection. Recent research has attempted to rectify this general concern through using an amalgamation of various historical threats, such as population density in 1500 A.D. (Gelfand et al., 2011; Mrazek et al., 2013), as well as historical pathogen prevalence (Fincher et al., 2008). Nonetheless, we fully agree that experimental research should be conducted

in tandem with correlational, cross-national research to form more conclusive claims.

Nevertheless, it is possible that a larger constraint on experimental research is that contemporary measurement of human behavior and underlying neurobiological mechanism does not comprehensively describe what the human mind and brain were like during historical times, when ecological pressures may have been more variable (e.g., due to limitations of existing technology). Scientific and technological change—for instance, the discovery of vaccines for infectious disease or new territories allowing for migration flow out of densely populated regions—represent notable milestones in the evolution of human civilization, yet are often not adequately modeled in empirical research examining culture and evolution or cultural neuroscience. More emphasis on modeling historical or archival data on existing ecological pressures during distinct historical epochs when cultural or genetic change may have occurred is an important and necessary endeavor for more accurately determining causal influences on culture and human evolution more broadly.

Further experimental research is also necessary to clarify the dynamic relationships between specific genes that exhibit strong psychological phenotypes and cultural traits and norms (Hong & Christopoulos, this issue; Sasaki, this issue). Sasaki (this issue) suggests that cultural priming (such as with religion) in Gene  $\times$  Environment studies can demonstrate whether people with particular allelic variants are more or less affected by the cultural prime within a given behavioral domain (such as prosociality). We highly encourage Gene  $\times$  Environment experiments to examine the interaction between effects of culture and genetic inheritance on brain and behavior. When conducting these studies, systematically choosing a control group that shares similar genetic makeup to Group A and similar cultural tendencies as Group B can create a triangulation method of comparing results that will help differentiate the influence of both culture and genotype as mentioned by Sasaki (this issue). Careful experimental methodologies such as this hold great promise for the field of cultural neuroscience. Furthermore, we advocate behavioral and neuroimaging studies that examine cultural influences on gene expression, such as DNA methylation, and the influence of epigenetic change on cultural norms, practices, and beliefs across levels of analysis. By examining the bidirectional dynamic influence of cultural and biological change on the mind and brain, we gain leverage on the question of causal influences in cultural difference.

Culture may exert causal influence not only on our genetic and neural makeup but also on our immune systems. Meyer et al. (this issue) suggest an innovative method to study the dual influence of culture and genes. Specifically, they suggest that inflammatory response may play a mediating role in the parasite-stress

theory, such that those with increased inflammatory activity demonstrate increased sensitivity in response to negative social cues relevant to ingroup/outgroup dynamics. This was demonstrated in their experimental work by administering a bacterial endotoxin, which was shown to increase inflammatory activity (Eisenberger, Inagaki, Rameson, Mashal, & Irwin, 2009; Inagaki, Muscatell, Irwin, Cole, & Eisenberger, 2011). To bridge this research with the culture–gene coevolutionary field, future research should examine how biological change, such as priming inflammatory response, varies as a function of candidate genes such as the serotonin transporter gene, as well as cultural inheritance. For example, if S allele carriers of the 5-HTTLPR polymorphism are more likely to show increased inflammatory response in reaction to pathogen prevalence, this would provide greater substantiation for the causal links in prior culture–gene coevolutionary research.

One fruitful way to study cultural neuroscience over a longer, generational time scale would be to examine immigrants and their families over several generations. This approach may help scientists unpack how genotypes change over time *within* a culture, opposed to between cultures. We agree with Gutchess and Goh (this issue) that this cross-generational approach holds great promise for understanding how culture-related factors shape allelic variation within families or genetic inheritance over time. We suggest that the source analysis approach should work in conjunction with the cultural mapping approach to more fully understand how and when culture and biology influence one another. Although genes often play an important role in this field, it is also possible for cultural experiences to directly influence brain activity independent of influences of genotype, as mentioned by Park (this issue). By tracking immigrants and their families, this approach would help scientists understand how neural plasticity responds to cultural change and life experiences. By studying immigrant parents (e.g., individuals who emigrated at a young age) who learn to become bicultural from distinct environments, and their children, who learn to become bicultural from a shared environment, with neuroscience methods, we will have a stronger test of the intersection between nature, nurture, and its interaction.

Finally, we would also like to suggest that future cultural neuroscience research across the lifespan would be beneficial in understanding how cultural acquisition forms and interacts with biology due to neuroplasticity and learning due to cultural entrainment. Both Christopoulos and Hong (this issue) as well as Freeman (this issue) mention research that epitomizes the influence of environment and cultural entrainment on neural structure. Specifically, they mention the work of Maguire and colleagues (1999) showing that licensed London taxi drivers having greater hippocampal

volume in relation to years of experience, as well as the work of Draganski and colleagues (2004), which demonstrates that the more juggling experience a juggler had, the more grey matter develops. Future longitudinal neuroimaging or cross-sectional neuroimaging designs (Park et al., this issue) may shed great insight into the timescale of neural plasticity in response to cultural learning and environmental factors. For example, neuroimaging could help illuminate how neural function, and perhaps neural structure, changes when individuals move from a rural neighborhood where they were born and raised to a large, urban city. Examining various changes across the lifespan, in turn, may help cultural neuroscientists use cultural mapping to facilitate the source analysis approach to better understand the question of why the world holds such immense behavioral variability.

### **The Adaptive Brain Shaped by Coevolution**

#### **The Mutual Adaptiveness of Culture**

A key theoretical premise of culture–gene coevolutionary theory is that cultural and genetic traits that are selected for serve adaptive functions (Boyd & Richerson, 1985). For instance, cultural values of collectivism may serve an antipathogen and antipsychopathology function, providing a set of behavioral repertoires that help people protect against the social transmission of infectious disease and a psychological buffer improving mental health (Chiao & Blizinsky, 2010; Fincher et al., 2008). Notably, once cultural and genetic traits are adaptive, mental and neural architecture are shaped to further facilitate these adaptive functions (Boyd & Richerson, 1985). Sasaki (this issue) calls for greater clarity in the concept of adaptiveness of cultural traits, with the distinction between adaptiveness in an evolutionary biology sense that defines adaptive traits as those that provide greater survival and reproductive fitness, and adaptiveness that describes the personal well-being, success, and health of individuals. Yet these two conceptualizations of the adaptiveness of cultural traits are not independent of each other, and may mutually constitute each other, as greater fitness afforded for the survival and reproduction of groups, societies, and populations by cultural traits also reflects advantages to well-being, health, success of individuals within those collectives.

In the broadest sense, cultural traits are adaptive in that they are malleable and function as a mechanism for individuals, groups, and populations to adjust to the demands of the shared contexts they are situated in. These cultural groups could be defined using diverse boundaries, such as social-economic status or religious traditions (see Sasaki, this issue) and are not merely limited to national or ethnic cultures. Rather,

when considering the adaptive nature of culture, cultural group boundaries could be conceptualized by exposure to shared contextual pressures and demands that require a set of normative and behavioral adaptations. For instance, although cultural groups may typically be defined by ethnic or national boundaries because members of such populations are influenced by similar geopolitical and regional factors, individuals of lower (or higher) social-economic status (see Stephens et al., 2007) may also be distinguished as cultural groups because they share similar constraints, pressures, and demands that exert converging influences on cognition and behavior, such as promoting interdependent self concepts.

The adaptability of culture can be observed through the dynamic of cultural knowledge to contextual affordances and constraints (Hong, Morris, Chiu, & Benet-Martinez, 2000; see Han, this issue; see Sasaki, this issue), such as to recurring situational demands (Oyserman & Lee, 2007), ecological threats and pressures (Gelfand et al., 2011; Triandis, 2009), or means of food and resource acquisition (Nisbett, 1990; Uskul, Nisbett, & Kitayama, 2008). Although one key function of culture may be to provide a basis for adjustment to systematic situational and environmental demands, whether any given set of cultural traits is indeed optimally adaptive is a different matter.

As Sasaki (this issue) mentions, the most normative cultural traits are not always the most adaptive ones, and we similarly advocate that cultural neuroscientists should not assume that the fluid, dynamic, and adaptable nature of culture will always provide the optimal solutions to resolving shared external pressures or dilemmas associated with group living. Next we briefly outline three reasons for why a given set of cultural adaptations may be maladaptive despite the overall function of culture to provide psychological and behavioral adaptations to contextual demands.

#### **Contextual Demands That Shape Culture Undergo Changes**

Like the cultural processes they shape, environmental demands and pressures are also fluid and changing. Natural and man-made changes to the shared environment, such as shifts in climate, abundance of resources (i.e., overfishing or overharvesting), population density, or medical and technological advances, can sometimes occur at drastic rates. Such changes can also alter how advantageous a set of cultural practices, values, or norms may be for well-being, survival, or reproductive success. But once cultural traits reach an equilibrium and become stable within a group, such traits may be self-sustaining and remain normative even after the initial pressures that prompted them are removed. As a consequence, some cultural practices may currently

appear to be maladaptive, even though they may have provided advantages in the past.

Consider, for example, the "culture of honor," or the socialization to norms promoting fierce and aggressive retaliation to perceived insults and slights to one's honor (Nisbett & Cohen, 1996). Such cultural norms are prevalent in historically pastoral societies, such as the American South, where aggressive responses to insults would have deterred others from absconding with one's livestock. In other words, a culture of honor may have served an adaptive function to the shared contextual pressures of exploitation faced by pastoralists, given the easy mobility of their resources. Yet despite its adaptive value for pastoralists of the past, the culture of honor that persists among the general non-pastoral population in the American South may be perceived as an unnecessary or maladaptive cultural trait, as this population no longer leads a pastoral lifestyle. In the modern era, heightened vigilance and aggression to perceived slights may lead to negative outcomes, such as personal harm, incarceration, or death. Similarly, other cultural norms that may appear maladaptive may be due to changes in the environmental pressures that may have initially prompted the adoption of those norms.

### **Migration and Immigration Into New Environments and Cultures**

Another mechanism in which cultural traits may appear to be maladaptive is in the context of migration. Just as environments may change over time and due to social and technological advances, environmental pressures may suddenly change as a result of migration. As individuals and populations migrate into new cultural environments, they bring with them existing cultural knowledge, practices, and strategies, which are applied to their host cultures. Cultural traits may undergo a dynamic process of change during acculturation (see Christopoulos & Hong, this issue; Park et al., this issue), in which existing cultural knowledge is reconciled with new social demands. Consequently, dominant practices and strategies among a group that were adapted to the demands of the home environment may appear maladaptive or to exhibit a "non-fit" when applied to a host culture or an environment with different demands and affordances.

For example, Cross (1995) found that among East-Asian students studying in the United States, those who exhibited greater levels of independent self-construal styles reported adopting more direct problem-solving strategies (culturally normative in the United States), which predicted lower levels of perceived stress. On the other hand, East-Asian students who exhibited greater levels of interdependent self-construal styles reported experiencing more stress during their adjustment to the United States. These findings reveal the impor-

tance of understanding the compatibility of cultural practices with the broader social environment. With the ever-increasing levels of migration, globalization, and multiculturalism across societies, cultural neuroscience should be aware of the roles that acculturation and cultural adjustment have on understanding the adaptive nature of culture.

### **Conformity to Cultural Norms (Even Maladaptive Ones) Can Offer Its Own Benefits**

Conformity to cultural norms can itself provide advantages for individuals, regardless of whether adherence to the norms provides any intrinsic value. As an inevitably interdependent species (Brewer, 2004; Brewer & Caporael, 2006), human beings must rely on group living and exchanges with group members as a primary adaptation and buffer against the challenges and threats posed by the external environment. Yet cooperation is parochial in nature, and is most often directed specifically at those who possess markers of ingroup membership (Efferson, Lalive, & Fehr, 2008; Hammond & Axelrod, 2006; Kurzban & Leary, 2001). Signaling or informing others of one's common group membership is a necessary component for benefitting from ingroup social exchanges (Yamagishi & Mifune, 2008; Yamagishi, Mifune, Liu, & Pauling, 2008). Consequently, abstaining from normative cultural practices may have signaled deviance, lower status, or untrustworthiness, which may have reflected that an individual was unfit as a social exchange partner, leading to social exclusion, punishment, and stigmatization (Cosmides & Tooby, 1992; Goffman, 1963; Kurzban & Leary, 2001). Furthermore, the adherence to cultural norms and the rejection of norm violators may have even greater importance in regions that faced greater ecological threats to survival and demanded higher levels of group cohesion (Gelfand et al., 2011).

Thus, conforming and participating in normative behavior may have served as a signal for common group membership, which would have afforded the benefits of group living, reciprocal social exchange, and cooperation. Even if culturally normative practices may ultimately have maladaptive or harmful consequences for their practitioners, they may still persist by serving as a signal for group membership and cultural identity. For instance, the Fore of Papua New Guinea have been documented to engage in ritualistic cannibalism of the dead, which consequently leads to the development of kuru, a neurodegenerative disease that usually results in death (Lindenbaum, 2008). Despite the harmful consequences of this practice for its practitioners, such practices may become customary given its relationship to the broader cultural identity of its practitioners. Moreover, adhering to more extreme (and potentially more maladaptive) cultural practices and norms may be more

effective for signaling group membership, identity, and cohesion, given that such practices are less likely to be common or shared with cultural outgroups.

In summary, how “adaptive” a cultural trait may be for individual well-being, success, and reproductive fitness cannot adequately be judged without taking into account the contextual demands to which the trait was adapted. Like culture, such contextual demands are also fluid and in a state of change; thus, although a given set of cultural practices may have promoted fitness and well-being in one context or at one point in time, the same practices may appear maladaptive when observed in another context. Furthermore, given the reliance of individuals on group membership for many fitness-relevant advantages (i.e., success, survival, reproductive opportunities), adhering to valued cultural practices and norms may serve as an adaptive response despite the negative personal consequences of such practices and norms.

### Conclusion

The notion that our brain inherits regulatory mechanisms not only from the genome but also from culture is still relatively new. There remains scant evidence for culture–gene coevolutionary theories of human brain and behavior; however, our impression is that this is largely due to limitations in attempts at empirical investigation, not in the capacity to uncover such evidence once such investigations are undertaken. The rapid progress in discovering convergent evidence for cultural influences on neural mechanisms as well as interactions of cultural and genetic processes in explaining human behavior demonstrates that the field of cultural neuroscience stands on firm ground.

Furthermore, developing regions of the world have not yet even begun their scientific journey into the human brain, due to economic or sociological constraints. Thus, we still do not yet understand fully the effects of geographic, economic, and sociological conditions in these regions on human brain development and evolution. When reminded of such circumstances, it is deeply fortunate that, nevertheless, great progress in cultural neuroscience has been made thus far. Notably, our comprehensive understanding of human nature is bound, at least in part, by increasing scientific inquiry and discovery across the globe, specifically in regions such as the developing world, due to the precious cultural and genetic variation that exists in the human populations that reside there. Although the early years of cultural neuroscience may feel especially swift, we do not doubt that cultural neuroscience is truly slow science. In many ways we have only just begun to unravel our neural ancestry, and each step forward brings us novel theoretical and empirical puzzles to collectively solve and savor.

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The first three authors contributed equally.

### Note

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