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REVIEW ARTICLE

Cultural neuroscience: new directions as the field matures

What do cultural neuroscience findings mean?

Luke W. Hyde · Steven Tompson · J. David Creswell · Emily B. Falk

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Abstract Cultural neuroscience has documented factors that affect biological and psychological processes that reciprocally shape beliefs and norms shared by groups of individuals. Here we highlight open questions regarding the stability versus malleability of these findings across time, environments, and cultural settings. By borrowing points from population neuroscience (Falk et al., in Proc Natl Acad Sci 110:17615–17622, 2013) and neurogenetics (Bogdan et al., in Mol Psychiatry 18:288–299, 2012), we highlight considerations for research on the development of differences in brain structure and function, particularly in the context of cultural variation. These points highlight the need to better understand gene by culture interactions; in particular, the potential role of ancestry, and the role the brain likely plays as a mechanism through which gene by culture interactions affect behavior. Moreover, we highlight the need to consider development in the interaction of culture and biology. We also highlight methodological challenges as neuroscience is brought to the population level including the importance of sampling and experimental equivalence across groups and cultures. In total, this discussion is aimed at fostering new advances in the young field of cultural neuroscience and highlighting ways in which cultural neuroscience can inform a broader understanding of the development of differences in complex behaviors.

L. W. Hyde (✉)
Department of Psychology, Center for Human Growth and Development, Institute for Social Research, University of Michigan, Ann Arbor, USA
e-mail: lukehyde@umich.edu

S. Tompson
Department of Psychology, University of Michigan, Ann Arbor, USA

J. D. Creswell
Department of Psychology, Carnegie Mellon University, Pittsburgh, USA

E. B. Falk
Annenberg School for Communication, University of Pennsylvania, Philadelphia, USA

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Introduction

The fields of human neuroscience and cultural psychology have each grown exponentially in the past two decades. With this growth, has come increased knowledge and specification in each field, as well as the creation of a field at their intersection—cultural neuroscience. At its core, cultural neuroscience has much to offer the broader neuroscience community, as well as much to gain from developments in other areas of neuroscience such as developmental, social, affective, and cognitive neuroscience (Cacioppo et al. 2000; Collins et al. 2001; Davidson and Sutton 1995; Goldsmith et al. 2008; Johnson 2010; Lieberman 2007; Ochsner and Lieberman 2001). Several thoughtful reviews have outlined examples of cultural neuroscience research and generated a research agenda for the field (e.g., Chiao et al. 2010; Han et al. 2013; Kim and Sasaki 2014). Our goal in the current paper is to highlight some ways in which the principles and lessons learned by pioneers in cultural neuroscience also apply to a wide range of questions in other areas of neuroscience, while pointing to ways in which cultural neuroscience can benefit by incorporating new ideas and approaches from other sub-fields. Specifically, we highlight ideas from work we have done in population neuroscience (Falk et al. 2013) and developmental neurogenetics (Hyde 2015) to inform our consideration of open question in cultural neuroscience.

In an effort to highlight bridges between subfields, we use a broad definition of culture as *factors that affect the biological and psychological processes that shape beliefs and norms shared by groups of individuals*. This inclusive definition has the advantage of highlighting both the socially constructed nature of who is and is not part of a group, and the ways that psychology and biology interact to shape experience. Such a definition also highlights the mutual benefits of dialog between cultural neuroscience and other subfields, as well as specific methodological and conceptual issues that will lead to more efficient advancement across subfields.

We begin first by highlighting selected key conceptual issues with models used to understand findings in cultural neuroscience. We consider the role that neural plasticity and development play in these models. Next, we focus more specifically on how such conceptualizations might apply to gene by culture interactions theoretically and the mechanisms through which these interactions shape behavior. Finally, we consider current methodological challenges in how (cultural) neuroscience is conducted and how insights from across areas of neuroscience might help bring together the conceptual challenges highlighted.

Conceptual challenges

We begin by considering how culture, as *factors that affect the biological and psychological processes that shape beliefs and norms shared by groups of*

individuals, gets under the skin. Early work in cultural neuroscience established several examples of culture × situation interactions (in the form of neural response) as well as gene × culture interactions. One major point for interpreting differences in cultural neuroscience is the extent to which brain findings are static versus the extent to which they may be malleable. At its core, this question requires deep understanding of biological mechanisms for brain plasticity, development, and neurogenetics, as well as thoughtful consideration of how culture interacts with each. Although solving this puzzle is clearly beyond the scope of this piece, in the following sections, we provide high-level overviews of some of the key issues inherent in studying each part of this question.

What role does brain plasticity play in the instantiation and manifestation of culture?

Although once believed to be relatively static, we now know that the brain undergoes considerable plasticity across development. For cultural neuroscience, this raises a key question regarding the extent to which observed group differences in neural response to tasks are permanent, heritable, and/or biologically transmitted across different cultures. That is, if we see differences in biology (e.g., neural function) across cultural groups, are we documenting heritable or permanent differences between these groups? Or are we documenting experience-dependent changes in brain structure and function?[1]

As cultural neuroscience has documented ways in which neural structure and function vary across major cultural groups (e.g., subgroups from eastern and western societies), we might ask how these differences arise. Social and cognitive neuroscience has documented how repeated engagement in daily tasks shape the ways that we use our brains and hence how they are built and function (Maguire et al. 2006). Such examples provide a window into the ways in which culture might take hold—the repeated practice of rituals and events within particular environments reinforces some biological and neural pathways and not others. Culture provides individuals with behavioral norms and scripts that direct how an individual is likely to behave in a given context or in response to a given task. Repeated engagement in these cultural practices reinforces neural pathways that are recruited in the accomplishment of these cultural tasks, which ultimately leads to changes in neural structure and/or function (Kitayama and Tompson 2010). For example, researchers have found that experts in using an abacus (a tool primarily used in Asian countries to perform arithmetic operations) recruit different brain regions when engaging in mental calculation than non-experts (Hanakawa et al. 2003), and thus the repeated experience of using a cultural tool such as an abacus to complete a given task can lead to fundamental changes in how our brain works. On the other hand, genetics play a role in shaping the types of rituals and practices likely to be enacted and sought out in the first place through active gene–environment

[1] Note that though we set-up dichotomies throughout this paper (i.e., are these changes experience dependent versus heritable), we do so only to highlight the questions in the field. As noted throughout, we believe that most, if not all, pathways we are discussing are clearly the product of interactions between the person and context.

correlations (e.g., many studies show that experiences, such as stressful life events are heritable, meaning that genes affect the environments we expose ourselves to; Kendler et al. 1995).

These points raise the important follow up question: If these changes are culturally experience-dependent, what level of stability do we expect? How long do we expect cultural changes or differences to remain at the behavioral level or at the neural level? Studies in the neuroscience literature highlight how behavioral training practices (e.g., juggling) can induce lasting changes in brain structure over the course of months (Draganski et al. 2004) and some recent studies suggest that long-term use of culturally embedded behavioral practices, like meditation, are associated with robust changes in neural structure and function (Creswell and Lindsay 2014). Likewise, the process of acculturation to a new environment almost certainly alters both brain structure and function over time and in ways that last year or decades. Theoretically, the longer that an individual is in their culture, the greater the extent to which this culture should alter their brain and behavior. For example, researchers have found that activation in neural regions involved in processing of visual scenes varies as a function of both culture and age. Specifically, both American and East Asian older adults (ages 60–78) recruited regions involved in processing of focal objects in a visual scene less than younger adults (ages 19–27), but American older adults showed a smaller decline in object processing than East Asian younger adults (Goh et al. 2007). Given research in cultural psychology that shows that East Asians tend to focus on focal objects less than Americans, the researchers argued that experience in East Asian culture and adoption of culturally normative basic cognitive processes (i.e., visual attention) leads to greater reductions in neural activation for East Asian older adults. Thus, cultural differences in basic cognitive and neural processes may actually increase as people get older (see below for more considerations related to development across the lifespan).

Although the above argument suggests that cultural influences on behavior, brain structure, and brain function may be chronic and long lasting, other research suggests that cultural effects may be enhanced or dampened depending on the situational context (Oyserman and Lee 2008; Sui and Han 2007). That is to say, even if immersion in a particular cultural context leads to fundamental changes in brain structure and function over longer periods of time, the extent to which these changes manifest themselves may depend upon the degree to which that cultural context is made salient and rendered important in any particular situation. Research on cultural priming has found that increasing the salience of one cultural identity can lead to more culturally normative patterns of thinking (Sui et al. 2007) and in turn influence neural activation (Ng et al. 2010; Sui et al. 2007).

The studies reviewed above highlight a need to consider how stable we expect culturally specific effects to be (i.e., does your brain change on a moment to moment basis over short time scales, as when one is on vacation, or does it take a prolonged level of acculturation to show effects?). The work reviewed above on longer term changes in brain function across the lifespan highlights potential interactions with age and developmental stage with effects of culture on the brain. From a practical standpoint, researchers interested in reconciling these issues have a number of potential options. First, the choice of who is studied (e.g., newly acculturated, only

those who were born and raised in a specific culture) may influence the results observed; specific reporting of this information will facilitate larger scale and aggregate (i.e., meta-analytic) approaches to answering some of the questions outlined above. Second, longitudinal studies that follow individuals as they develop could test the ways in which specific momentary influences (e.g., priming) interact with longer term developmental influences, which are discussed in greater detail in the next section. Third, as noted below, studying individuals at different developmental and acculturation stages could help to uncover the ways in which length of experience and development interact to affect the stability of these neural changes.

What role does development play in the neural embedding of culture?

In considering the dynamic interaction of brain and culture across an individual's life, it may be useful to consider the trajectory of development and how development plays a role in the neural embedding of culture. For example, at what ages do different types of cultural experiences play a role in behavior and in brain development and in what ways might cultural norms, values and practices be more or less plastic over time? Behavioral studies have shown that understanding of concepts like culture, race, and ethnic identity vary across development (Baron and Banaji 2006; Seaton et al. 2006). Language acquisition is a concrete example of the role of development in the effects of culture and the brain. For example, research has shown sensitive periods in which children first make and can distinguish sounds from all languages but that over time are only able to make and distinguish sounds from their own language (Werker and Tees 2005). Interestingly, in this case, it seems as though a child tuning into his or her own language's sounds is adaptive for learning language more quickly (Kuhl 2010). These behavioral differences are measurable at the neural level with different processing patterns for different languages (Kovelman et al. 2011; Kuhl 2010; Petitto et al. 2012).

As a second example, later in development, adolescents become highly sensitive to social cues, which, in turn, alters brain function. For example, adolescent reward systems may be sensitized in the presence of peers (Chein et al. 2011), with peers creating distinct subcultural influences. This influence is likely specific to adolescence as peer influence is not as important in earlier childhood and these brain systems are not in as rapid a period of maturation. Thus, in adolescence, peers may be a particularly salient cultural influence, especially as this is a period of greater brain maturation in the reward system.

More generally, throughout the lifespan, developmental stage can shape social interactions that form the basis for learning and creating culture (defined by shared norms and values), but the relevant brain systems and cultural factors may change across development. As such, neuroscience that explores differences between adolescents and children or adults, do not only study the "effect of age" but also a different ecological or cultural context for these groups. Much research in ecological theory and developmental psychopathology has emphasized the embedding of individuals within a wider social context (Bronfenbrenner and Ceci 1994) and the continual transaction between individual and "context", which clearly

includes culture at multiple levels (Sameroff 1995). Models from these fields (Cicchetti and Toth 2009; Hyde et al. 2015), including Sameroff's transactional model (Sameroff 2009, 2000), emphasize the two way interaction between a developing child and their environment. Key to the transactional model is that the child actively shapes his or her own environment, sometimes as much as the child is shaped by this environment. Thus, though we may often conceptualize culture as influencing a child's developing brain, we must also conceptualize the child and individuals as shaping their own exposure to culture and culture as a whole, both at an individual level (i.e., a teenager may pick different peers which may lead to different cultural exposures; e.g., Dishion et al. 1996) and at the group level (for a description of a simliar process described by cultural psychologists see Markus and Kitayama 2010; Shweder 1991). Thus, brain-culture interactions are likely to be dynamic both across an individual's lifetime, as well as across historical time due to the co-evolution of culture and the brain (Kim and Sasaki 2014). Therefore, layered on top of the cultural groups and affiliations that shape our norms and values, the weight given to different identities and cultural referents changes across the lifespan, due to differential effects of culture at difference ages and due to effect of age and corresponding brain development on subcultural influence and visa versa. Models that explicitly account for development are critical if we are to begin to understand how culture is biologically imbedded across situations and developmental stages. More broadly, the role of development will be key to understanding mechanisms and the unfolding of brain-culture relationships. As we note below, cultural neuroscience models that examine more complex models (e.g., gene–culture–brain) can help to accurately capture the complexity of brain-culture relationships, and these models will need to incorporate development to examine how these relationships may vary during different developmental periods (e.g., gene–culture–development interactions).

How do we understand gene by culture interactions?

As we move toward a deeper understanding of the broad interaction between biology and culture, and the degree to which cross-cultural differences are malleable, one specific conceptual challenge concerns the extent to which differences found in neuroscience are due to culture versus genetic background or ancestry. There are now a wealth of Gene by Culture (G × C) interactions demonstrating that the relationship between a specific genetic allele and behavior is moderated by culture or conversely that cultural differences are moderated by specific genetic alleles which may make individual more or less susceptible to cultural influences (Kim and Sasaki 2012; Kitayama et al. 2014). For example, people born and raised in the United States are, on average, more likely to have an independent social orientation than people born and raised in East Asia, but these cultural differences are greater for carriers of specific alleles within a dopamine receptor gene (i.e., DRD4; alleles thought to result in higher dopamine-signaling and increased reward sensitivity) (Kitayama et al. 2014). Likewise, carriers of specific alleles in the oxytocin receptor gene (i.e., ones thought to enhance socio-emotional sensitivity) are more likely to show the culturally dominant patterns of

emotion regulation, such that Asians with the allele are more likely to use suppression as a regulation strategy and less likely to engage in emotional support seeking, whereas Americans with the same gene variant are more likely to use support seeking (Kim and Sasaki 2012). These types of results have been interpreted by cultural neuroscientists as demonstrating culture's influence on the expression of underlying neural phenotype from gene differences (see more below on neural mechanisms of G × C), or alternatively as markers of those more or less sensitive to the environment/culture (Kim and Sasaki 2014). However, key to this interpretation are a few assumptions. First, is that the same allele is having the same effect on cellular and neural physiology across cultural groups, which may not necessarily be true. Much of how we know the "functionality" of different alleles is from animal models, which assume homology with humans and that humans are homogenous in this physiological sense. However, we know people of different cultural backgrounds differ in physiology (e.g., prevelance of lactose tolerance; Beja-Pereira et al. 2003). These basic physiological differences can be attributed to differences in diet, behavior, and geographic location, but one major source is likely to be genetic differences attributable to different genetic ancestry (Fujimura and Rajagopalan 2011; Shriver and Kittles 2004).

To extend this argument, if a G × C interaction is observed, is culture truly moderating the genetic effects, or is the allele in question differentially correlated with other alleles that systematically vary by ancestry and thus culture? In this case, a G × C interaction may reflect a latent gene by gene interaction effect that is correlated with different allele frequencies across different cultural groups. In fact, human geneticists go to great lengths to avoid genetic substructure or to control for the effect of ancestry when mapping genetic variation to behavior due to these concerns (Cardon and Palmer 2003; Freedman et al. 2004). Conversely, emerging work in animals models has begun to suggest that epigenetic changes that are due to experience and affect gene expression may be passed between generations (Meaney 2010). If this mechanism persists in humans across generations (McGowan et al. 2009), then what appear to be G × C interactions, could also reflect longstanding epigenetic C × C interactions.

To address such issues, cultural neuroscience can use thoughtful designs to separate out the effects of genetic ancestry from the effects of culture, or more broadly to isolate "true" genetic versus "true" environmental effects. This point is particularly important since genes and cultures in G × C interactions are likely to be correlated and difficult to separate without innovative designs. The challenge of separating what are "genetic" versus what are "cultural" effects is akin in some ways to separating out gene–environmental correlations in individual differences research (Manuck and McCaffery 2010). As with gene–environment correlation and interactions, genes and culture are highly confounded and likely interacting and shaping each other over time. Gene × Environment interaction studies have employed genetically informed designs such as twin and adoption samples (Reiss and Leve 2007), as well as natural experiments (Costello et al. 2003; Kilpatrick et al. 2007), to identify true "environmental" effects (Jaffee 2011). Cultural neuroscientists might consider similar methods that leverage twins (e.g., monozygotic twins with identical DNA that are raised in different cultures), adoption (e.g.,

comparing those adopted within or outside of a culture but who had similar ancestry) or natural experiments to better understand G × C interactions.

Beyond possible twin or adoption designs, researchers could use acculturation and movement of those with similar ancestry into new cultures. For example, researchers might compare first or second-generation immigrants in one country with those still in their native country and those in the new country. In this example, researchers could study second or third generation Chinese-American's who are still genetically "Chinese" but are more likely to be culturally "American". This group could then be contrasted with native Chinese who share ancestry, but not culture, and European-American's who share culture but not ancestry (or even another recently immigrated group who would share acculturation stress and discrimination, as well as American cultural orientation, but not ancestry). This type of design illustrates one way to partially separate out these two highly correlated factors (i.e., culture, genetic ancestry), either of which could be driving G × C interactions. However, this example also highlights the difficulty of separating out these effects. In this example, third generation Chinese-Americans may have very low exposure to Chinese culture, but genotypic variations associated with Chinese ancestry could lead to systematic differences in the types of situations and environments that these Chinese-Americans self-select into or expose themselves to than European-Americans. Moreover, even though both European- and third generation Chinese-American individuals are both situated within the same "American" culture, they may spend time in different subcultural groups (e.g., via peers with more similar cultural backgrounds) and the cultural environment may respond to these individuals differently leading to qualitatively different "cultural" exposures (i.e., exposure to the same general culture does not necessarily equate to similar experience among the two groups). Ultimately, separating out these two possible effects will be difficult but is important to understand the extent to which these interactions reflect true cultural versus genetic influences.

What is the mechanism of gene by culture interactions?

Given recent working highlighting gene by culture interactions (Kim and Sasaki 2012, 2014; Kitayama et al. 2014) and the moderating effect of culture on many brain-behavior links (Chiao et al. 2010; Han et al. 2013; Hyde et al. 2011), an emerging emphasis in cultural neuroscience will be merging brain–culture and gene–culture interactions into broader integrative models. One framework that may be useful in integrating these strands of research is an Imaging Gene by Environment (IG×E) approach (Hyde et al. 2011) that has come out of work in neurogenetics (Bogdan et al. 2012) and developmental neurogenetics (Hyde 2015). This recently proposed model, highlights neural structure and function as the mediator of Gene × Environment (G × E) interactions. Conversely, this model can also be seen as specifying an imaging genetics model (i.e., a model in which genetic variablity predicts variability in neural structure and function; Munoz et al. 2009) that is moderated at multiple levels of context or experience (Bogdan et al. 2012; Hyde 2015). Culture can be conceptualized as forming one important "environment" within this model (though note that culture may differ from other

"environments" in that exposure to a specific culture does not necessarily guarantee socialization or enculturation to the culture). To the extent to which culture can be conceptualized as an "environment", this affords relatively straight-forward translation of concepts to a model in which culture moderates the effect of genetic variation on brain structure and function and subsequent differences in behavior. As noted in these neurogenetics models, one way in which the culture likely interacts with genetic variation at the molecular level is through alteration of gene expression and epigenetic mechanisms (Cole 2009; Hyde et al. 2011; Meaney 2010). By applying this neurogenetics approach, cultural neuroscientists might seek to model IG×C pathways where gene by culture interactions are linked to behavior via their effect on brain structure and function (see Fig. 1). These interactions with culture can happen at two stages: (1) between genes and culture in affecting brain function, and (2) between culture and brain function in affecting subsequent behavior. Although there may be some instances where genetics and culture directly influence behavior, the IG×C model suggests that a key pathway through which biological and cultural factors influence behavior is through brain function. Thus, effects of

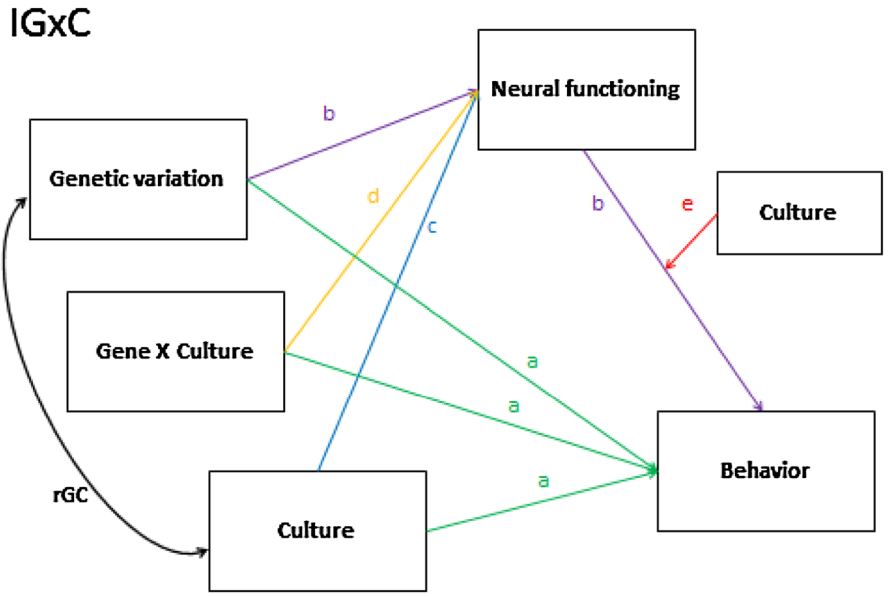

Fig. 1 Integrating culture into an Imaging Gene by Environment Model: Imaging Gene by Culture Interactions (IG×C). This figure represents a conceptual and statistical model of an imaging gene by environment interaction (Hyde et al. 2011) in which culture is seen as an all-encompassing environment, presented two different ways for ease of interpretation. Note that both *panels* denote the same model. In this model, gene by culture (G × C) interactions are modeled as having their effect on behavior via their effect on the brain. *Green paths* marked with A represent a G × C interaction. *Purple paths* marked with B represent a model in which genes linked to neurotransmission are linked to behavior via their effect on brain structure or function (imaging genetics). The *blue path* marked with C note that likely effect of cultural differences on differences on brain structure and function. The *yellow path*, marked with D, represent the conditional relationship of genetic variation on brain structure and function where culture moderates this pathway. Finally, the *red path* marked by E represents the moderating effect of culture on brain-behavior links. (Color figure online)

brain function on behavior at the second stage can also be driven by genetic factors or by the interaction between genetic and cultural factors. Moreover, effects of genetics and culture on behavior can be mediated by changes in brain function. For example, differences in serotonin genes may only affect amygdala reactivity if these genes are being expressed at certain levels and in certain brain areas (Cole 2009). If cultural experiences affect this level of gene function, then a G × C interaction (Kim et al. 2010) could subsequently affect amygdala reactivity (i.e., culture moderates the effect of genetic variability on brain function and thus on subsequent behavior). As another example, from literature described above, individuals with specific alleles within the dopamine receptor gene may alter dopamine signaling and subsequent neural response in reward structures (e.g., striatum, prefrontal cortex). These neural changes may make individuals more sensitive to acquiring cultural differences (Kitayama et al. 2014), but only in those with these alleles and subsequent differences in neural response to reward (i.e., genetic variability affects neural function and subsequent behavior but is moderated at the brain-behavior level via culture). As this example illustrates though, it is important for those doing work on G × C interactions, to begin to hypothesize or measure neural mediators. That is, genes to not simply make individuals "more plastic" or "more sensitive". Genes code for proteins that can affect neural structure and function, which may eventually lead to individual differences in response to the environment and culture. Thus, a next step forward for G × C research is to examine the biological mechanisms mediated these interactions.

Furthermore, culture may also be seen in the IG×E model as a further moderator of IG×E pathways. That is, the effect of a certain experience on brain function and its interaction with genotype may vary depending on cultural context. For example, genetic variation in the stress system may be a marker for those more susceptible to traumatic events and thus interact with trauma to affect brain and behavior (Bogdan et al. 2012; White et al. 2012). However, what constitutes trauma or the effect of a traumatic event may be moderated by the cultural norms of the group and/or characteristics of the environment shaped by culture (e.g., religion, social support; Ellison 1991; Stephens and Long 1999). Thus, IG×E models could be seen as being further moderated by culture. These types of links can be estimated statistically through moderated mediation models and likely represent the more complex and realistic nature of the interaction between genes, culture, the brain and behavioral outcomes (for more details on statistical approaches and challenges of these models see Hyde et al. 2011). Overall, these models offer a way of linking cultural neuroscience work focusing on neuroimaging and behavior with gene by culture interaction work focusing on the conditional effects of genes and culture. They may also help to push the field of cultural neuroscience to specify the underlying mechanisms through which G × C interactions are instantiated biologically.

Methodological challenges

The examples above highlight several open questions in cultural neuroscience and human neuroscience more broadly regarding the balance of biology and culture in

shaping behavior and experience. Inherent in each of the issues noted above is the extent to which biology and behavior observed in one context (e.g., developmental phase; genetic environment) generalize to others within the organism. We next turn to conceptual and methodological issues inherent in constructing theories of human behavior that account for variation both within and between cultures.

An exchange with population neuroscience: how does culture moderate brain effects?

One major finding from cultural psychology and cultural neuroscience is that findings from psychology and neuroscience do not necessarily generalize to all people. In other words, one brain is not the same as the next brain (e.g., there is not one "representative" brain; Ceci et al. 2010; Chiao and Cheon 2010; Henrich et al. 2010). Much of the existing corpus of human neuroimaging research uses convenience and snowball sampling, often on college student populations. Thus, much of what we know about "the brain" is actually based on collegiate and middle-class American and Western European brains (Falk et al. 2013), who differ in many concrete ways from others within America and those in the rest of the world (Chiao and Cheon 2010; Henrich et al. 2010).

Importantly, however, culture moderates brain-behavior relationships (Chiao et al. 2010). In parallel with studies demonstrating the dangers of convenience sampling, cultural neuroscience findings highlight the need to attend to *who* is being studied in all fields of neuroscience (for a more detailed discussion of this point and population neuroscience see Falk et al. 2013). For example, neural responses to even basic affective neuroscience tasks such as exposure to emotional faces (Hariri et al. 2000), vary by culture (Chiao et al. 2008), as do basic cognitive responses to geometric figures (e.g., Kitayama et al. 2003). These differences are likely due to differences in perception and interpretation of the stimuli by those in different cultures (e.g., the tendency to view geometric figures by their parts or holistically which varies by cultural background). Thus, it is not only cultural neuroscientists (e.g., studying eastern versus western cultures) who must be mindful of potential group differences; a robust understanding of the phenomena treated by social, cognitive, developmental, and affective neuroscience requires addressing the possibility of neural and psychological variation even within subcultures in the same local region, such as higher versus lower SES and urban versus rural cultures.

Likewise, though cultural neuroscience findings have been critical to highlighting the need for a population neuroscience perspective, the field of cultural neuroscience itself would benefit from even greater incorporation of a population neuroscience approach. For example, many cultural neuroscience studies contrast those in one culture (e.g., East Asians) to another culture (e.g., Americans). However, the samples themselves are often of college or university students in each country/culture, which could lead to the building of much knowledge in cultural neuroscience on samples that vary by country that are still restricted in their range. For example, a recent paper found large-scale psychological differences (i.e., levels of interdependence versus independence) within China that were explained by rice versus wheat production; this example highlights that within an "eastern" and

"interdependent" culture, there is wide psychological heterogeneity (Talhelm et al. 2014). Just as cultural neuroscience has expanded the bounds of human neuroscience to include cross-national comparison groups, recent work within cultural psychology now pushes cultural neuroscience to compare sub-cultures within nations.

From a practical standpoint, there are several ways that researchers can take steps to reconcile these issues, which are treated in greater detail in our recent manuscript focused on "Population Neuroscience" (Falk et al. 2013). For example, subsampling from larger population studies, development of data sharing and consortium models, and cross-site collaboration are three methods that balance these goals. Indeed, there is not one set of characteristics that should be captured more representatively—instead, the culturally-informed theory, research question, and the population(s) to which researchers wish to generalize must guide the sampling plan. In other words, neither the tenets of cultural neuroscience nor population neuroscience mandate that researchers create a representative sample of the entire world population or of the country they are in, but rather to be thoughtful about (and explicitly sample for and report) who comprises the target population and how findings may be moderated by sample composition (for more suggestions on ways to address this challenge see Falk et al. 2013). Increased reporting of such logic as well as sample characteristics will facilitate later meta-analytic comparisons that may be beyond the reach/resources of any individual study team.

How can data be collected in a way that is culturally sensitive and equivalent across groups?

Cultural neuroscience has also developed a nuanced treatment of environmental cues, task and stimulus meaning. Importantly, the same stimulus might have very different interpretations and emotional consequences for one group relative to another. For example, work by Chen and colleagues has demonstrated that lower SES adolescents interpret ambiguous social cues as more threatening and show corresponding physiological stress reactions to cues perceived as neutral or positive by their higher SES counterparts (Chen et al. 2004; Chen and Matthews 2001, 2003). Thus, an issue that is both practical and theoretical for cultural and population neuroscience is how to make fMRI tasks that are equivalent across cultures. For example, participants from Western and Eastern cultures might respond differently to persuasive messages beginning with the words "You should…" versus "Let's all…", the former sounding more natural to those from more individualistic Western cultures and the latter more natural to those from more collectively oriented Eastern cultures. In this context, a researcher would be faced with the decision of whether to make stimuli match in literal translation or in familiarity. One solution might be to split the difference and have half of the phrases in a study sound natural for each group, thus allowing the research team to test for possible interactions. Acknowledging and documenting such variation is essential for constructing a more complete picture of the neural correlates of emotion, cognition, and behavior (e.g., see Chiao et al. 2010). Indeed, although researchers

may wish to control or reduce such variation under some circumstances, such differences may also provide fruitful research foci.

As one example that goes beyond simply understanding how people from different cultural backgrounds might interpret the same instructions in different ways, research has documented that the language in which the participants complete the task can have a large impact on how people think and behave. For example, bilingual Chinese individuals studying in Canada describe themselves in more independent ways and report valuing independence more when filling out surveys in English than in Mandarin (Ross et al. 2002) and bilingual Chinese students in Hong Kong tend to judge themselves as being more positive, less susceptible to moral transgressions, and more likely to distance themselves from a peer who did better on an exam when asked in Chinese than in English (Lee et al. 2010). These effects suggest that bilingual individuals will behave or respond in ways that are more normative in Western cultures when prompted in English and respond in ways that are more normative in Asian cultures when prompted in Chinese. This may be due to a priming effect, such that speaking in English activates knowledge of Western culture whereas speaking in Cantonese activates knowledge of Chinese culture.

Our broad definition of culture as *factors that affect the biological and psychological processes that shape beliefs and norms shared by groups of individuals* also points to the fact that such issues apply not only when translating language across cultures, but also when 'translating' tasks or stimuli for groups who speak the same language. For example, equivalent task instructions might be interpreted differently by participants from lower and higher SES backgrounds, by those from different racial groups, by younger and older participants, and by participants from different geographic regions who subscribe to different shared norms. What might be a simple categorization task for some could represent a social stressor for another, and the complexities raised above with respect to nuanced biological and broader environmental factors apply strongly here as well. As an example, neural responses to emotional faces (Hariri et al. 2000) varies not only by culture (Chiao et al. 2008), but also by race within the same culture (Lieberman et al. 2005) and in response to pictures of people within an in-group versus out-group (Hart et al. 2000). Notably, these differences could be due to cultural differences in early perceptual processing of faces, or also one's culturally-learned subsequent interpretation or valuation of these faces. Indeed, there is initial evidence that culture modulates neural responses in both early processing (e.g.. early perceptual face processing: Ratner et al. 2014; Sui et al. 2013) and later interpretation or valuation (e.g., empathic valuation: de Greck et al. 2012). As another example, it may be very difficult to assess neural response to reward (e.g., Knutson et al. 2000) across those from different socio-economic strata because the value of a specific reward (e.g., $20) may vary by participant based on their own resources and needs. More generally, the instructions used to describe tasks, as well as the task content and context can signal to participants that the task (and potentially broader study) are designed for someone "like me" or "not like me", which in turn may interact with genetic sensitivities and developmental stage. Though this methodological point may be obvious within cultural neuroscience, it may be under-appreciated more broadly in neuroscience. This point highlights the

importance of moving toward population neuroscience models with samples and sample sizes that are capable of documenting differences and constructing integrative theories that traverse levels of analysis in diverse groups of people. Again, depending on the core research questions, it may be desirable to control or reduce such variation, or to capitalize on it to understand specific cultural phenomena.

Other sources of variation (e.g., differences in scanner physics across sites), however, may be less interesting from a cross-cultural stand point, but rather introduce noise into investigations and therefore must be appropriately addressed. As human neuroscience scales up and seeks more representative, more diverse, and larger samples, it is essential to minimize certain types of potential differences when collecting data across sites—that is, as we move towards a more population focused neuroscience, how can we collect data across groups and sites that are equivalent on dimensions that aren't the core focus of study? This point is particularly important when site may be confounded by a variable of interest, such as culture, geographic location, or nationality. For example, an fMRI study comparing Japanese and American subjects living in their respective countries might require an MRI facility in each place. Though there have been great strides in cross-site scanner calibration and equivalence (Fennema-Notestine et al. 2007; Glover et al. 2012; Sutton et al. 2008), any "noise" introduced by site is confounded by culture. Moreover, to bring subjects all to the same scanner poses equal problems in that it may make one group travel farther or experience the scanning environment differently. Beyond challenges with scanner equivalence, one must also consider other technical challenges in subsequent MRI imaging processing across cultures, such as the need for culturally appropriate brain templates (Chiao et al. 2010). These questions have traditionally not been considered as deeply by researchers outside of cultural neuroscience who have primarily opted to collect data locally but are important as emerging studies span larger collections of people across different countries (e.g., the IMAGEN project which spans across several european countries; Schumann et al. 2010). Explicit consideration of such factors in the technical design of studies also stands to benefit social, cognitive and developmental science more broadly.

Conclusions

Cultural neuroscience is an exciting and relatively new inter-disciplinary field that has significant potential opportunities and challenges. We have shown how gene × culture, developmental neurogenetics, and population neuroimaging approaches can inform (and be informed) by this area. We argue that the challenges are two-fold. First, we advance four conceptual issues for neuroscientists to consider when examining the role of culture. Specifically, we consider the potential stability (or lack of stability/malleability) in cultural neuroscience effects, and the extent to which culture and brain may interact across development. Next, we highlight the need to separate influences of culture versus ancestry on behavior. Given that the mechanism through which gene by culture interactions affect behavior is likely through the brain, this affords new ways of approaching the conceptual questions

highlighted, but also suggests broader methodological challenges for human neuroscience more broadly. In this vein, cultural neuroscience can push other subdisciplines of human neuroscience to consider methodological challenges such as sampling and the effect of culture on task/experimental conditions, while cultural neuroscience can consider ways to broaden beyond focusing on group based differences between groups that may not be representative. Through a greater interchange between subfields of human neuroscience, we can build a better, more representative knowledge base of the development of differences in behavior and the role culture plays in the development of these complex behaviors.

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