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CHAPTER 20

Cultural neuroscience: a once and future discipline

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Abstract: The study of culture and biology has long stood stratified within the social and natural sciences, a gap that physicist C.P. Snow (1959) famously called "the two cultures." Cultural neuroscience is an emerging, interdisciplinary field that examines the bidirectional influence of culture and genes to brain and behavior across multiple timescales. Integrating theory and methods from cultural psychology, brain sciences, and population genetics, cultural neuroscience is the study of how cultural values, practices and beliefs shape brain function and how the human brain gives rise to cultural capacities and their transmission across macro- (e.g., phylogeny, lifespan) and micro timescales (e.g., situation). The current article presents the aims and methods of cultural neuroscience, highlights recent empirical findings in the field, and discusses the potential implications of this field for bridging the social and natural sciences as well as informing interethnic ideology and population health concerns, more broadly construed.

Keywords: cultural neuroscience; culture; brain; fMRI; ERP; culture–gene coevolution; transcultural neuroimaging

Introduction

> Why are the tribes and nations of the world different, and how have the present differences developed? — Franz Boas (1907)

The nature and origin of human cultural diversity has been a rich source of intellectual curiosity for scholars since the first millennium. Early in the 7th century, Isidore of Seville observed in one of the earliest written encyclopedias, *Etymologiae*, that humans vary both in physical appearance and ways of thinking (Jahoda, 2002). Centuries later, philosophers, such as Descartes and Locke, renewed debate on the origin of human diversity in thinking and behavior. During the Age of Enlightenment, the study of human diversity accelerated with the emergence of two enormously influential, but divergent, schools of thought: evolutionary biology and modern anthropology. Darwin's theory of evolution led to the development of the field of evolutionary biology, which explained diversity in the biological world as emerging from the universal process of natural selection. By contrast, pioneering anthropologists, such as Franz Boas and Margaret Mead, favored scientific approaches to culture that emphasized relativism whereby human cultures were best understood on their own terms, rather than as products of transparent universal laws, including those of a biological nature (Lewis, 2001).

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Following Darwin and Boas, the scientific study of biology and culture largely continued to diverge, even with the emergence of nexus fields, such as psychology, which would appear well-positioned to formally integrate theory and methods across the social and natural sciences. Evolutionary psychologists, for instance, argue that the human mind and behavior are best understood as adaptations or functional products of natural selection and embrace neuroscience as a means uncovering universal neural circuitry specialized for solving different adaptive problems (Barkow et al., 1992). Widely adopted by modern cognitive neuroscientists, this evolutionary approach to the study of the human brain has proved enormously fruitful for generating sound hypotheses and evidence for how discrete brain structures map onto distinct kinds of adaptive psychological functions (Caramazza and Shelton, 1998; Dehaene and Cohen, 2007; Kanwisher et al., 1997). However, this evolutionary emphasis has also steered much scientific attention within cognitive neuroscience toward the study of universal, rather than culturally specified, neural mechanisms and behavior. By contrast, cultural psychologists have largely focused on investigating the mutual constitution of culture and the human mind and have convincingly constructed theories and discovered evidence that culture shapes nearly every facet of psychology and behavior (Kitayama and Cohen, 2007). However, as a consequence, cultural psychologists have spent less time thinking about how to meaningfully integrate theories of human culture with theories of human evolution and how cultural values, practices, and beliefs shape not only mental, but also neurobiological, processes.

The past century has witnessed a number of theoretical attempts within psychology to integrate cultural and neurobiological approaches in the study of the human mind and behavior. For instance, prominent developmental psychologists, such as D'Arcy Thompson and C. Waddington, introduced early notions of probabilistic epigenesis, whereby humans come into the world with sets of possible developmental trajectories that are then pursued or not over the course of the lifespan as a result of interactions with the cultural environment (Johnson, 1997). More recently, biocultural co-constructivism theory has emerged as a way of explaining how developmental trajectories unfold via interactions between genetic and cultural factors, and importantly, how neural plasticity may later both developmental trajectories and the end state (Li, 2003).

Despite rich theoretical motivation for studying culture–biology interactions within the human brain, precise empirical demonstrations and theoretical models of bidirectional relationship between cultural and biological mechanisms (e.g., culture–gene; culture–brain; culture–brain–gene) have largely remained elusive. A number of factors have contributed to the current knowledge gap. First, empirical studies of neural substrates underlying human emotion and cognition have typically been informed first by empirical evidence in non-human animals (Davidson and Sutton, 1995; Gazzaniga et al., 2002). However, since cultural competence is predominantly a human achievement (Dehaene and Cohen, 2007; see also, Tomasello et al., 2005) it is not possible for behavioral neuroscience models of culture to inform human neuroscience investigations of culture. Second, until recently, researchers have lacked technology to study these questions in humans. For instance, the field of human neuroimaging began to flourish only within the past two decades (Fig. 1a). Third, there is typically a lack of awareness among researchers about the growing research bias in the populations that they study (Arnett, 2008). Within the field of psychology, 95% of psychological samples come from countries with only 12% of the world's population (Arnett, 2008). Within the field of human neuroimaging alone, 90% of peer-reviewed neuroimaging studies come from Western countries (Fig. 1b). Moreover, a growing number of critical neuroscientists are beginning to document how such researcher biases affect how neuroscientists construct theories and design future experiments (Choudhury et al., 2009). Hence, our current state of knowledge of mind–brain mappings is largely restricted to scientific observations made of people living within Western industrialized nations, leaving a large empirical gap in our

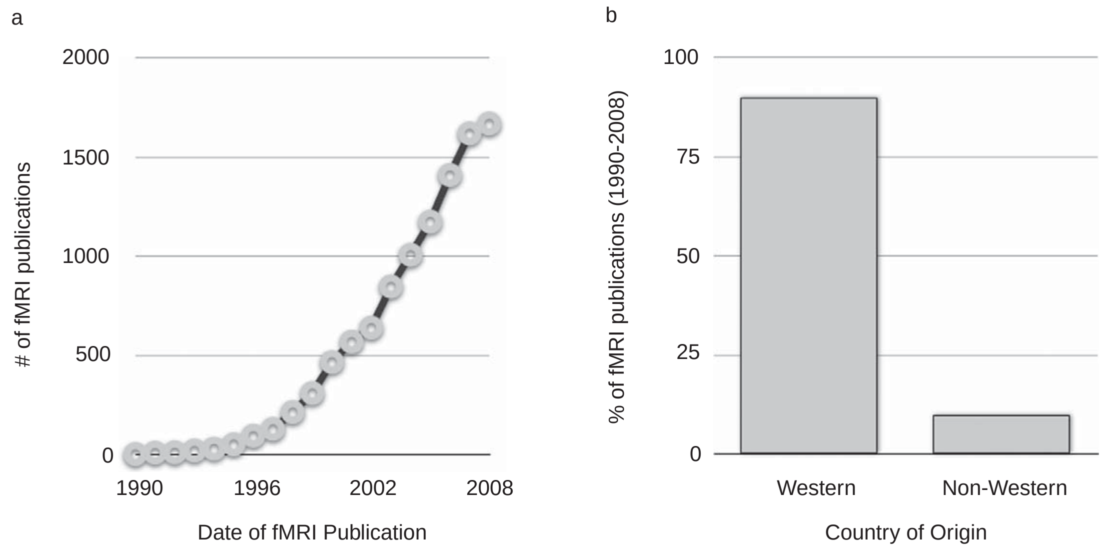

Fig. 1. Growth trends and publication bias in peer-reviewed human neuroimaging literature. (a) Graph illustrating the growth in peer-reviewed human neuroimaging studies from 1990 to 2008; (b) graph illustrating the publication bias within the human neuroimaging literature whereby the vast majority (~90%) of publications to date originate from a Western country.

understanding of how diverse cultural environments affect the human mind, brain, and behavior.

What is cultural neuroscience?

Cultural neuroscience is an emerging research discipline that investigates cultural variation in psychological, neural, and genomic processes as a means of articulating the bidirectional relationship of these processes and their emergent properties (Fig. 2). Research in cultural neuroscience is motivated by two intriguing questions of human nature: how do cultural traits (e.g., values, beliefs, practices) shape neurobiology (e.g., genetic and neural processes) and behavior and how do neurobiological mechanisms (e.g., genetic and neural processes) facilitate the emergence and transmission of cultural traits?

The idea that complex behavior results from the dynamic interaction of genes and cultural environment is not new (Johnson, 1997; Li, 2003; Caspi and Moffitt, 2006); however, cultural neuroscience represents a novel empirical approach to demonstrating bidirectional interactions between culture and biology by integrating theory and methods from cultural psychology (Kitayama and Cohen, 2007), neuroscience (Gazzaniga et al., 2002), and neurogenetics (Canli and Lesch, 2007; Green et al., 2008; Hariri et al., 2006). Similar to other interdisciplinary fields such as social neuroscience (Cacioppo et al., 2000) or social cognitive neuroscience (Ochsner and Lieberman, 2001), affective neuroscience (Davidson and Sutton, 1995), and neuroeconomics (Glimcher et al., 2008), cultural neuroscience aims to explain a given mental phenomenon in terms of a synergistic product of mental, neural, and genetic events. Cultural neuroscience shares overlapping research goals with social neuroscience, in particular, as understanding how neurobiological mechanisms facilitate cultural transmission involves investigating primary social processes that enable humans to learn from one another, such as imitative learning. However, cultural neuroscience is also unique from related disciplines in that it focuses explicitly on ways that mental and neural events vary as a function of culture traits (e.g., values, practices, and beliefs) in some meaningful way. Additionally, cultural neuroscience illustrates how cultural traits may alter neurobiological and psychological processes beyond those that facilitate social experience and behavior, such as perception and cognition.

Why study cultural influences on brain function?

There are at least three reasons why understanding cultural and genetic influences on brain function likely holds the key to articulating better psychological theory. First, a plethora of evidence from cultural psychology demonstrates that culture influences psychological processes and behavior (Kitayama and Cohen, 2007). To the extent that human behavior results from neural activity, cultural variation in behavior likely emerges from cultural variation in neural mechanisms underlying these behaviors. Second, cultural variation in neural mechanisms may exist even in the absence of cultural variation at the behavioral or genetic level. That is, people living in different cultural environments may develop distinct neural mechanisms that underlie the same observable behavior or recruit the same neural mechanism to varying extents during a given task. Third, population variation in the genome exists, albeit on a much smaller scale relative to individual variation, and 70% of genes express themselves in the brain (Hariri et al., 2006). This population variation in allelic frequency in functional polymorphisms, such as those that regulate neural activity, may exert influence on subsequent mental processes and behavior. To the extent that behavior arises from neural events and both cultural and genetic factors influence neural events, a comprehensive understanding of the nature of the human mind and behavior is impoverished without a theoretical and empirical approach that incorporates these multiple levels of analyses.

Theory and methods in cultural neuroscience

The current ability to discover cultural variation across multiple levels of analysis is now possible in ways never previously imagined, due in large part, to fortuitous theoretical and methodological advances in three distinct fields: cultural psychology, brain sciences, and neurogenetics (Figs. 2 and 3). In recent years, cultural psychology has made major advances in identifying cultural traits that characterize the diversity in social groups around the world as well as articulating the criteria for creating culturally appropriate behavioral measures that ensure the psychological phenomena of interest is testable in people of all cultures (Kitayama and Cohen, 2007; Norenzayan and Heine, 2005). Human neuroscience, including cognitive, social, and affective neuroscience, has revolutionized the study of the mind and brain by developing an arsenal of techniques for mapping neural

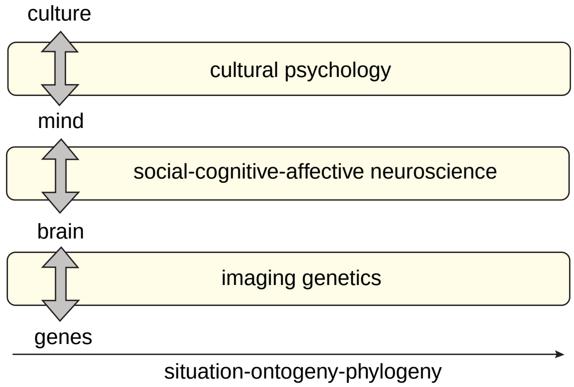

Fig. 2. Illustration of the cultural neuroscience framework, integrating theory from cultural psychology, social/cognitive/affective neuroscience, and neurogenetics.

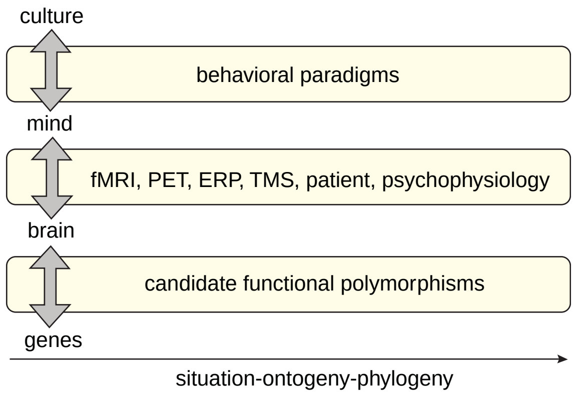

Fig. 3. Illustration of the cultural neuroscience toolbox, integrating methods from cultural psychology, social/cognitive/affective neuroscience, and population genotyping.

processes to psychological processes at varying degrees of spatial and temporal resolution (Gazzaniga et al., 2002; Handy, 2005; Heeger and Ress, 2002). Molecular biology has witnessed major transformations in the scope of data and techniques now available for understanding the structure and function of the human genome. From techniques for studying the association between single genes and behavior to genome-wide maps that assess the association of the entire genome to a given behavior, the development of molecular biology techniques has led to an explosion of possible ways for mapping genes to neural, mental, and cultural processes. Taken together, the convergence of these tools enables unprecedented ability to investigate the mutual constitution of genes, brain, mind, and culture.

Cultural psychology

Theory and methods of cultural psychology comprise the first component of the cultural neuroscience toolbox. First, cultural psychologists have developed rich set of theoretical constructs that specify what kinds of cultural values, practices, and beliefs reliably impact human behavior. For instance, Hofstede (2001) proposed that cultures could be distinguished according to five cultural dimensions: *individualism–collectivism*, *uncertainty avoidance*, *power distance*, *long-term/short-term orientation, and masculinity/femininity*. The cultural dimension of *individualism–collectivism*, in particular, has been shown to reliably affect a wide variety of human mental processes at a behavioral level, including self-concept, motivation, perception, emotion, and cognition (Markus and Kitayama, 1991; Triandis, 1995). Individualism refers to when individuals construe themselves as separate and autonomous from each other, whereas collectivism refers to when individuals construe themselves as highly interconnected and defined by their relations and social context. Another potent cultural construct is *holistic* versus *analytic cognition*, a dimension thought to characterize differences in thinking styles between Westerners and East Asians. East Asians are thought to primarily engage in holistic cognition, attending to the entire field of a scene and relying on dialectical reasoning, whereas Westerners have been shown to primarily exhibit analytic cognition, attending to objects more than their context and using rules, such as formal logic, to understand reason about themselves and the world (Nisbett et al., 2001). Finally, *socio-economic status or social class* has been shown to serve as an important cultural lens shaping one's sense of free will, choice, and related behaviors (Snibbe and Markus, 2005; Savani et al., 2008). These cultural dimensions provide a core theoretical foundation from which cultural neuroscientists can formulate novel hypotheses about how and why culture may influence brain functioning. Formulating sound hypotheses about how cultural traits modulates neural mechanisms a priori is critical to building better theories about how culture shapes neural systems and why as well as ensuring that evidence of cultural variation in neural systems is not misinterpreted as evidence for essentialist theories of race (Tate and Audette, 2001).

Second, cultural psychologists have developed a number of novel behavioral methods for investigating cultural influences on behavior. First, a popular and effective way of measuring cultural traits is via *behavioral surveys*. Indeed, a lion's share of prior cultural psychological research has been focused on creation and validation of cultural value surveys, such as those used to measure individualism and collectivism (Singelis, 1994). Importantly, cultural psychologists have discovered that people living in diverse cultural value systems demonstrate different types of response biases when completing behavioral surveys. For instance, collectivists tend to show moderacy biases, such that they respond to items using the midpoint of Likert scales, whereas individualists tend to show extremity biases, such that they typically respond to items using the endpoints of Likert scales (Heine, 2008). Understanding when and how these response biases may emerge is critical for cultural neuroscientists wishing to map cultural variation in behavior to cultural variation in neural functioning.

Another important cultural psychological method is *situational sampling*. One of the hardest challenges in designing cross-cultural experiments is in ensuring that one's experimental stimuli have the intended meaning across cultures. Situational sampling refers to a technique for generating experimental stimuli that are optimized to reveal cultural variation in behavior. In experiments utilizing situational sample, researchers ask participants from the two or more cultures of interest to generate example of the phenomena of interest. Then, these examples are used as stimuli in a subsequent experiment to test cultural variation in responses to the culturally specific stimuli (Heine, 2008).

A third cultural psychology technique important for conducting cultural neuroscience research is *cultural priming* (Hong et al., 2000; Oyserman and Lee, 2008). Often, cross-cultural psychologists conceptualize nation or race as a proxy for culture; however, such gross characterizations of culture are impoverished as they fail to capture the individual variability within cultures, the dynamic nature of culture, and the fact that an individual can possess awareness of and appreciation for than one cultural system simultaneously. To address these important issues, cultural psychologists have developed cultural priming techniques to directly manipulate cultural value systems within mono- and multicultural individuals and to show how cultural values dynamically shape behavior. Cultural priming involves temporarily heightening individuals' awareness of a given cultural value system through either explicit (e.g., writing an essay about individualism) or implicit means (e.g., search for synonyms of individualism in a word search). A number of different types of cultural priming techniques have been successfully used to elicit cultural variation in a range of behavioral processes. Notably, prior research has revealed that not all cultural priming techniques have equivalent influence across domains; that is, some cultural priming methods are more likely to trigger cultural variation in social relative to cognitive processes and vice versa (Oyserman and Lee, 2008). Hence, when adopting cultural priming to study the direct influence of cultural values on neural mechanisms, it is important to select a cultural priming technique that is task-appropriate.

Human neuroscience

Cognitive neuroscience theory and methods comprise the second component of the cultural neuroscience toolbox. Recent decades have brought an unprecedented array of tools for directly and indirectly measuring human brain activity and relating this brain activity to behavior. There are several neuroscience tools that psychologists can use to map neural structure to mental function such as the following: functional magnetic resonance imaging (fMRI), positron emission topography (PET), transcranial magnetic stimulation (TMS), magnetoencephalography (MEG), event-related potentials (ERP), and lesion studies. Each tool has its strengths and weaknesses, particularly when comparing each tool's spatial and temporal resolution (Cacioppo and Decety, 2009). Neuroimaging techniques, such as fMRI and PET, record indirect neural activity and have very good spatial resolution (mm^3), but poor temporal resolution (seconds), relative to electrophysiological techniques such as ERP and EEG. By contrast, ERP and EEG record neural activity directly below the scalp and thus have excellent temporal resolution (milliseconds), but lack high spatial resolution. Newer hybrid techniques, such as MEG, combine the advantages of both brain imaging and electrophysiological techniques and it is likely that as medical technology improves, so will our ability to accurately record neural activity while awake humans perform mental tasks.

In addition to taking into consideration the spatial and temporal resolution of human neuroscience techniques, it is equally important to consider what kinds of questions can be addressed with each technique, and what questions remain unaddressed given the limitations of current methodologies. TMS and lesion studies enable researchers to address which brain regions are necessary for a given mental function, while brain imaging and electrophysiology provide tools for associating a given neural structure or processes to a given mental function. To date, most cultural neuroscience research has utilized cross-cultural or transcultural neuroimaging to demonstrate cultural variation in the magnitude of neural response to a given stimuli (Chiao and Ambady, 2007; Han and Northoff, 2008; Park and Gutchess, 2006). However, future research may also include novel methodologies, such as cross-cultural TMS or lesion studies, that will be able to address novel questions such as whether or not a given brain region is necessary for a given mental function in one culture, but not another.

Neurogenetics

The theory and methods from neurogenetics comprise the third component of the cultural neuroscience toolbox. Genes are the fundamental physical and functional unit of heredity. Genes substantially influence every level of human biology, including regulating neurotransmission within the brain. Recent advances in neurogenetics have led to major advances in our understanding of how genes regulate brain mechanisms underlying cognitive (Green et al., 2008), emotional (Hariri et al., 2006), and social behavior (Canli and Lesch, 2007).

Cultural variation is evident in the human genome for a number of reasons, albeit on a much smaller scale relative to individual genetic variation. Cultural variation in allelic frequencies of a given gene may occur due to number of evolutionary processes, such as natural selection and genetic drift. Natural selection may lead to differential frequency of gene variants when certain genetic variants confer reproductive advantages over another. Genetic drift may also result in changes in allele frequencies within populations over time, but in a more random manner. For instance, founder effects, a type of genetic drift, can lead to a loss of genetic variation when a new population is established by a very small number of individuals from a larger population.

Due to their robust allelic variation across cultures, two genes are likely to play a key role in future cultural neuroscience research: the serotonin transporter polymorphism (*5-HTTLPR*) and dopamine D4 receptor (*DRD4*) exon III polymorphism. The 5-HTTLPR consists of a 44-base pair insertion or deletion, generating either a long (l) or a short (s) allele. Evidence from behavioral genetics indicates that the S allele of the serotonin transporter gene (*5-HTTLPR*) is associated with increased negative emotion, including heightened anxiety (Munafò et al., 2005; Sen et al., 2004), harm avoidance (Munafò et al., 2005), fear conditioning (Lonsdorf et al., 2009), attentional bias to negative information (Beevers et al., 2007), as well as increased risk for depression in the presence of environmental risk factors (Caspi et al., 2003; Taylor et al., 2006; Uher and McGuffin, 2008, see also Munafo et al., 2009). In particular, exposure to chronic life stress, such as interpersonal conflict, loss, or threat, is considered a well-known environmental risk factor for depression in S allele carriers of the 5-HTT (Caspi et al., 2003). The s allele of the *5-HTTLPR* is extremely prevalent in East Asian populations (e.g., 70–80% s carriers) relative to other nations (e.g., 50% or less s carriers) (Chiao and Blizinsky, 2009; Gelernter et al., 1997). The dopamine D4 receptor (*DRD4*) exon III polymorphism has been linked to novelty seeking and pathological gambling (Chen et al., 1999). Individuals with the 7-repeat allele have higher novelty seeking scores than those with other *DRD4* variants (Chen et al., 1999). The 7-repeat allele is extremely prevalent in South American Indian populations (e.g., 70–80% 7-repeat carriers), but extremely rare in East Asian populations (e.g., $<1\%$ 7-repeat carriers) (Chen et al., 1999).

Importantly, genes not only regulate brain mechanisms and behavior, but also influence and are influenced by cultural selection (Boyd and Richerson, 1985). According to culture–gene coevolutionary theory, cultural traits can possess evolutionary advantages. For instance, cultural traits, such as individualism and collectivism (Fincher et al., 2008), may serve adaptive functions and thus, culturally consistent phenotypes may become selected for over successive generations, leading to population variation in allelic frequencies for certain genes. Additionally, a central claim of culture–gene coevolutionary theory is that once cultural traits are adaptive, it is likely that genetic selection causes refinement of the cognitive and neural architecture responsible for the storage and transmission of those cultural capacities (Boyd and Richerson, 1985). Hence, these evolutionary processes of cultural and genetic selection likely result in cultural variation in psychological and neural processes, which serve as endophenotypes or intermediate phenotypes of the cultural and genetic traits.

A central goal for cultural neuroscience research is to understand how these dual forces of cultural and genetic selection shape brain function and behavior. The field of neurogenetics provides the empirical means by which cultural neuroscientists can investigate similarities and differences in how genes regulate human brain function across cultures. More specifically, neurogenetics research enables cultural neuroscientists to identify neural endophenotypes or brain regions that may be influenced by culture–gene coevolutionary forces. For example, recent imaging genetics research has shown that people who carry the s allele of the *5-HTTLPR* exhibit greater amygdala response to emotional stimuli (Hariri et al., 2002) which is likely due to increased amygdala resting activation (Canli et al., 2005) and decreased functional coupling between the amygdala and subgenual cingulate gyrus (Pezawas et al., 2005), relative to individuals carrying the L allele. Future research in cultural neuroscience may examine the effect of cultural and genetic selection on amygdala response and emotional behavior. More broadly, by converging theory and methods from neurogenetics and cultural psychology, cultural neuroscientists are equipped to generate and test novel hypotheses not only about how genes or culture independently influence brain function, but also how genes and culture interact and mutually shape brain function across the lifespan and across successive generations.

Cultural influences on brain function: progress in cultural neuroscience

Not only does the human brain support the transmission of cultural values, beliefs, and practices via neural mechanisms of imitation (Iacoboni, 2009; Reynolds-Losin et al., in press), culture also dynamically shapes brain function across multiple timescales (Ambady and Bharucha, in press; Chiao and Ambady, 2007; Chiao, in press; Han and Northoff, 2008; Park and Gutchess, 2006; Wexler, 2006). Given the rich existing literature on how the brain facilitates cultural transmission (Iacoboni, 2009; Reynolds-Losin et al., in press), this next section will highlight illustrative empirical advances of the latter, namely how cultural values, beliefs, and practices influence neural mechanisms supporting a range of psychological domains, from perception and memory to emotion and social cognition.

Visual perception

Cultural beliefs, such as self-construal style, have been shown to influence visual perception at a behavioral level, as demonstrated by the Frame-Line Test (FLT) (Kitayama et al., 2003). The FLT measures one's capacity to both incorporate and to ignore contextual information in a non-social domain. Prior cultural psychology research has shown that people living in a collectivistic culture, such as Japan, are better at incorporating contextual information during perception of a focal object (e.g., relative condition) while people living in an individualistic culture, such as North America, are better at ignoring contextual information (e.g., absolute condition) when perceiving a focal object (Kitayama et al., 2003). These results suggest that cultural beliefs affect how a simple visual percept, such as a vertical line, is perceived and experienced.

Modulation of visual experience by cultural beliefs is thought to arise from frontal-parietal regions associated with high-level attentional modulation, rather than early stage primary perceptual processes associated with temporo-occipital regions (Hedden et al., 2008). Using fMRI, Hedden et al. (2008) measured neural activity while people completed a modified version of the FLT task. During scanning, people were asked to perform vertical line size judgments that involved either incorporating (relative condition) or ignoring (absolute) contextual information, such as the relationship between the perceived size of the line and the surrounding square frame. Brain imaging results showed that people recruited frontal and parietal regions associated with attentional control to a greater extent when engaged in a task that was incongruent with their cultural values. More specifically, neural activity in frontal-parietal regions increased when people of East Asian descent ignored contextual information and people of European descent incorporated contextual information during line size judgments. Moreover, degree of activation during the incongruent relative to the congruent judgments was negatively correlated with degree of individualism in people of European descent and degree of acculturation in people of East Asian descent. Hence, conscious perception of a vertical line embedded in a square frame and its underlying neural circuitry is affected by experience with and identification to a given cultural context.

Recent studies using ERP have found converging evidence of cultural values of individualism–collectivism on neural substrates of visual perception. In one study, Lewis et al. (2008) measured ERP while participants completed the oddball task, where they are shown visual stimuli in either a frequent or infrequent (i.e., oddball stimulus) manner. Results demonstrated that European-American participants showed greater novelty P3 amplitude for target events, whereas East Asians showed greater P3 amplitude to. In another study, Lin et al. (2008) recorded electrophysiological activity in extrastriate cortex while participants primed with either individualism or collectivism viewed compound visual stimuli in either a global or a local fashion. Results demonstrated that individualistic self-construal priming resulted in greater P1 amplitude during local relative to global processing, whereas collectivistic self-construal priming resulted in greater P1 amplitude during global relative to local processing. These results provide a novel demonstrate that temporarily heightening one's awareness of cultural values can dynamically alter neural responses during visual perception. Taken together, these findings provide convergent evidence that cultural values of individualism and collectivism modulate neural and electrophysiological responses during visual perception at both macro and micro timescales.

Memory

Cultural variation in holistic versus analytic thinking styles affects how people encode and retrieve information. Several cultural psychological studies have shown that Westerners are more likely to encode and retrieve focal objects in a complex visual scene, whereas East Asians encode focal and contextual information (Chua et al., 2005; Nisbett and Masuda, 2003; Nisbett et al., 2001). Recent cultural neuroscience evidence suggests that cultural variation in memory performance may occur, in part, to cultural variation in neural processing within lateral occipital regions, particularly in elderly populations (Gutchess et al., 2006; Goh et al., 2007). One cross-cultural neuroimaging study found that East Asians and Westerners vary within object-processing regions such as bilateral middle temporal gyrus (Gutchess et al., 2006). Another neuroimaging study comparing young and elderly East Asians and Westerners found that activity within the right lateral occipital region differed between East Asian and Western elderly, but not East Asian and Western young adults, providing novel evidence that neural regions may show cultural variation as a function of age (Goh et al., 2007).

Emotion

Culture shapes how people prefer to experience, express, recognize, and regulate their emotions (Mesquita and Leu, 2007). East Asian experience low arousal relative to high arousal positive emotions (Tsai, 2007), are more likely to suppress their emotions relative to Westerners (Butler et al., 2007). Additionally, both East Asians and Westerners demonstrate cultural specificity in emotion recognition, whereby they show greater recognition for emotions expressed by own cultural group members relative to members of other cultural groups (Elfenbein and Ambady, 2002). Recent cultural neuroscience of emotion research has shown cultural specificity effects

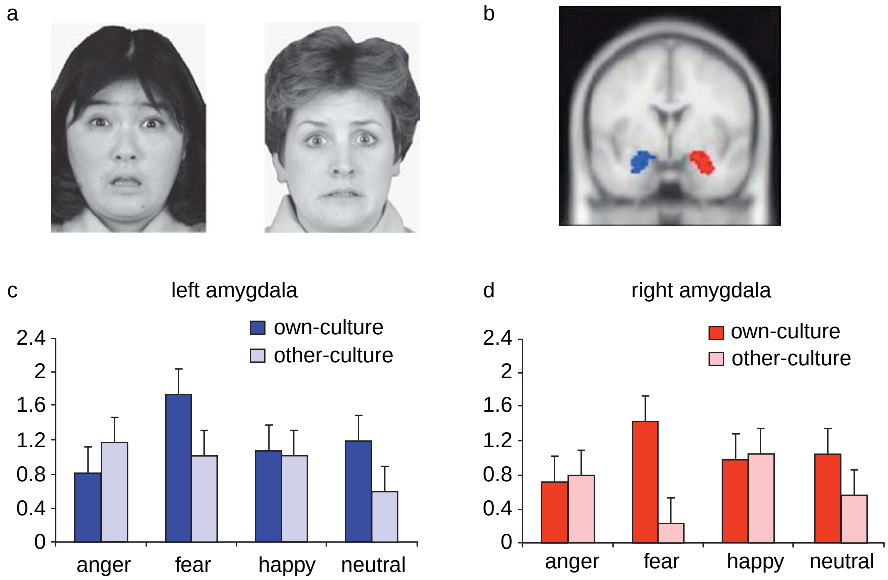

Fig. 4. Cultural specificity in bilateral amygdala response to fear faces (adapted with permission from Chiao et al., 2008b). (a) Examples of Japanese and Caucasian-American fear faces; (b) illustration of bilateral amygdala; participants show greater left (c) and right (d) amygdala response to fear expressed by members of one's own cultural group.

within a number of brain regions involved in emotion recognition. Consistent with prior behavioral findings, one recent study showed that both native Japanese and Caucasian-Americans exhibit greater amygdala response to fear faces expressed by own-relative to other-culture members (Chiao et al., 2008a, b, Fig. 4). Taken together, these findings provide convergent evidence that culture influences how people infer emotional states from nonverbal cues, and their underlying neural substrates, possibly by tuning neural responses toward familiar stimuli in the environment during development.

Another way that culture may affect affective neural response is by affecting its magnitude. Using cross-cultural neuroimaging, we have recently discovered a *cultural variation* effect in bilateral amygdala response to emotional scenes (Chiao et al., 2009c, in press). Caucasian-American (CA), Japanese-American (JA), and native Japanese (JP) participants, all of whom carried the S allele of the *5-HTTLPR* serotonin transporter gene, were studied using fMRI at 3T while they performed an emotion and cognitive inhibition task. Native Japanese S allele carriers showed significantly greater amygdala response relative to Japanese-American and Caucasian-American S allele carriers. Native Japanese S allele carriers showed significantly greater amygdala response relative to Japanese-American and Caucasian-American S allele carriers. Furthermore, there was no significant difference in amygdala response to emotional scenes between Japanese-American and Caucasian-American S allele carriers, suggesting that ethnicity of the participant is not a possible explanation for the difference between Native Japanese and Caucasian-American participants. By contrast to the emotion task, there was no significant main effect of cultural group in bilateral VLPFC response during inhibition. Our neuroimaging findings show that culture exerts a significant influence on bilateral amygdala response to emotional scenes, controlling for related genetic and racial factors.

Interpersonal perception

Recent cultural neuroscience evidence indicates that cultural group membership provides an important means by which people infer the mental states of others from nonverbal cues. The superior temporal sulcus (STS) is a region within the temporal lobe that transforms perceptual cues from the face, such as eye gaze direction and body orientation, into information about the goals and intentions of another (Nummenmaa and Calder, 2009). A recent neuroimaging study found that people exhibit STS activity when inferring the intentional states specifically from the eye region of others from their own-relative to other-culture (Adams et al., in press). These findings suggest that activity within STS processes culturally familiar percepts to a greater extent, possibly leading to greater mental state inference for own-relative to other-culture group members. Another recent study found that activity within the mesolimbic system responds more for culturally congruent dominant and submissive facial cues (Freeman et al., 2009). Individuals from egalitarian cultures, such as the United States, show greater mesolimbic response to dominant facial cues whereas individuals from hierarchical cultures, such as Japan, show greater mesolimbic response to submissive facial cues. Future research may examine whether cultural specificity in STS response results neural tuning within the lifespan toward familiar percepts, whether cultural values shape neural responses when forming first impressions of others from nonverbal cues as well as whether or not cultural reliance on display rules modulates cultural specificity or variation in response to nonverbal cues.

Social cognition

Cultural values, practices, and beliefs shape social behavior in profound ways. One of the most robust ways that values, such as individualism and collectivism, influence human behavior is in self-construal, or how people think about themselves in relation to others. Individualists think of themselves as autonomous form others, while collectivists think of themselves as highly interconnected with others (Markus and Kitayama, 1991; Triandis, 1995). Recent cultural neuroscience evidence indicates that neural substrates of self-knowledge and self-awareness are modulated by cultural values of individualism and collectivism (for review, see Chiao et al., 2008a). Evidence from social neuroscience indicates that specific brain regions, such as the medial prefrontal cortex (MPFC) and posterior cingulate cortex (PCC) are involved in self-evaluation and self-knowledge (Amodio and Frith, 2006). In one study, Caucasians, but not Chinese, showed greater neural activity within the MPFC during evaluation of personality traits of one's self relative to a close other (i.e., mother), suggesting cultural variation in MPFC response during self-evaluation (Zhu et al., 2007). More recent evidence has demonstrated that cultural values (i.e., individualism–collectivism), rather than cultural affiliation (i.e., East Asian–Westerners) per se, modulate neural response during self-evaluation. In one cross-cultural neuroimaging study, people in both Japan and the United States who endorsed individualistic values show greater MPFC activity for general relative to contextual self-descriptions, whereas people who endorsed collectivistic values show greater MPFC for contextual relative to general self-descriptions (Chiao et al., 2009a, Fig. 5). Supporting this view, another study using cultural priming showed that even temporarily heightening awareness of individualistic and collectivistic values in bicultural individuals (i.e., Asian-Americans) modulates MPFC and PCC in a similar manner (Chiao et al., 2009b, Fig. 6). Taken together, these studies provide convergent evidence that cultural values of individualism–collectivism shape neural representations of self-knowledge.

Additionally, cultural values of individualism and collectivism can moderate neural mechanisms underlying self-awareness. In a recent neuroimaging study examining self-construal style and neural correlates of self-awareness, Sui and Han (2007) primed participants with either an individualistic or a collectivistic self-construal style and then presented them with facial images of themselves, a familiar other or a scrambled face. Once the facial image was presented, participants were asked to indicate the head orientation of the intact face or the location of a gray bar next to the scrambled face. Greater activation within the middle frontal cortex was found for self relative to familiar and scrambled faces in the individualistic prime group while greater activation within the middle frontal cortex was found for both self and

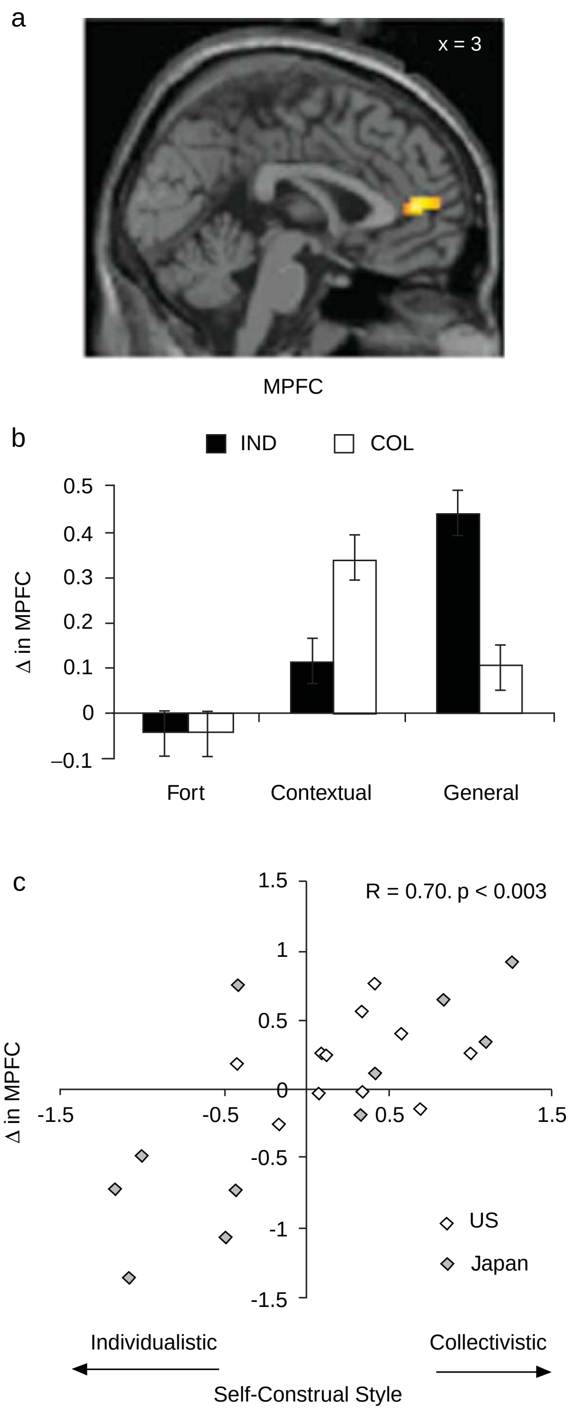

Fig. 5. Neural basis of individualistic and collectivistic views of self (adapted with permission from Chiao et al., 2009a). (a) Cultural values of individualism and collectivism modulate activity within medial prefrontal cortex (MPFC). (b) In both the United States and Japan, participants who endorse individualistic cultural values show greater MPFC response to general relative to contextual self-descriptions. Participants who endorse collectivistic cultural values show greater MPFC response to contextual relative to general self-descriptions. (c) Irrespective of nationality, the degree to which a person endorses individualistic or collectivistic values is positively correlated with neural activity within MPFC to general relative to contextual self-descriptions, respectively.

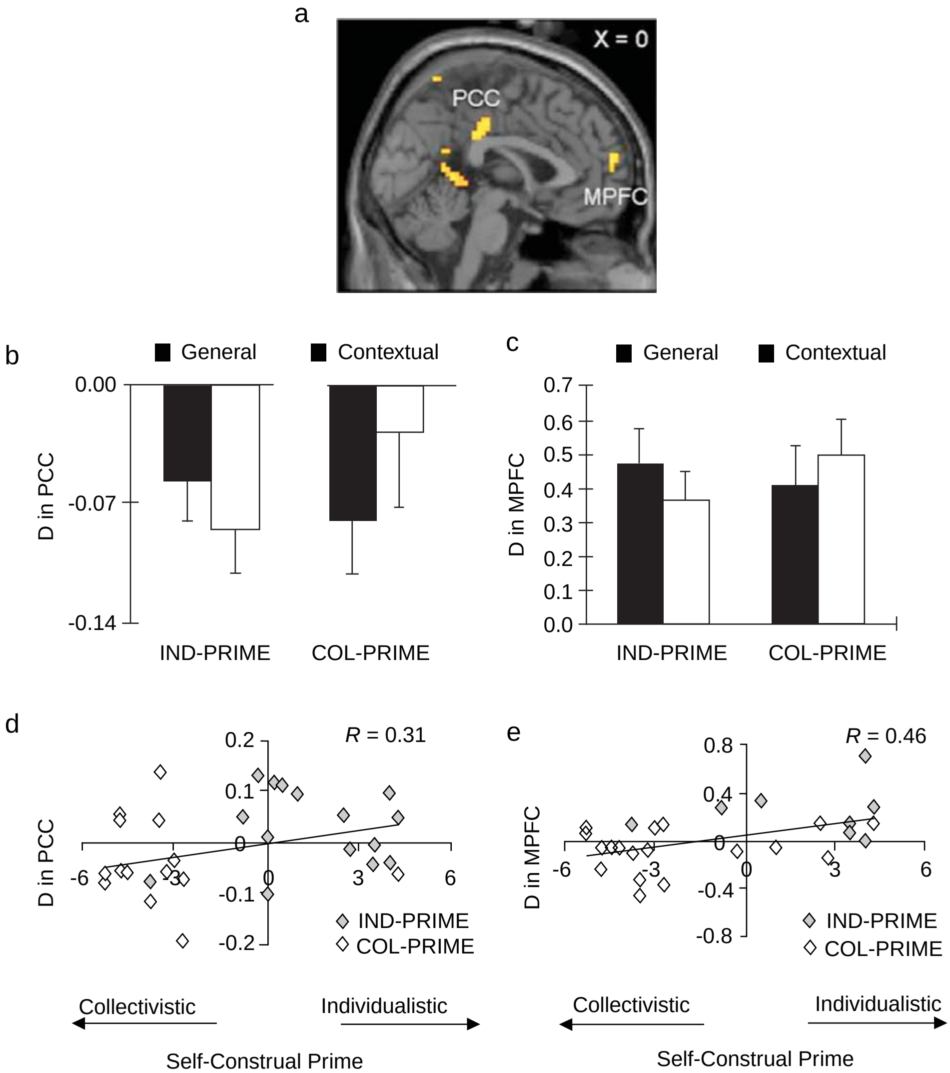

Fig. 6. Dynamic cultural influences on neural representations of self (adapted with permission from Chiao et al., 2009b). (a) Modulation of neural activity within cortical midline structures, including the posterior cingulate cortex (PCC) and medial prefrontal cortex (MPFC) as a function of cultural priming. Bicultural participants primed with individualistic cultural values show greater PCC (b) and MPFC (c) to general relative to contextual self-descriptions. Bicultural participants primed with collectivistic cultural values show greater PCC (b) and MPFC (c) response to contextual relative to general self-descriptions. The degree to which a person is primed with individualistic or collectivistic values is positively correlated with neural activity within PCC (d) and MPFC (e) to general relative to contextual self-descriptions, respectively.

familiar faces relative to scrambled faces in the collectivistic prime group. This modulation of neural activity by self-construal style was not present in other brain regions activated during the task, such as the right fusiform gyrus, a region critical to face processing. Hence, these results highlight the influence of cultural values on neural activity during self-awareness.

Finally, religious beliefs also play an important role in modulating neural responses underlying social cognition. One set of neuroimaging studies examining the neural substrates of religiosity found activity within theory-of-mind regions, including left precuneus, left temporoparietal junction, and left middle frontal gyrus was correlated with the degree of one's religiosity (Kapogiannis et al., 2009). Additionally, religious practices, such as praying, also modulate neural responses within theory of mind regions. For instance, compared to formalized prayer and secular cognition, improvised praying activated the temporopolar region, MPFC, temporoparietal junction, and precuneus (Schjoedt et al., 2009). Finally, religious beliefs affect neural representations of the self. Whereas atheists typically recruit ventral MPFC during self-evaluation, religious individuals show greater response within dorsal MPFC, suggesting that religious beliefs promote greater evaluation, rather than representation, of one's self (Han et al., 2008). Hence, the human ability to possess religious beliefs and exercise religious practices relies on theory-of-mind and mentalizing brain regions that facilitate the representation and evaluation of own and others (e.g., human, God) mental states.

Implications of cultural neuroscience for basic and applied research

It is not expected that the study of all psychological and biological phenomena will necessitate a cultural neuroscience approach. Rather, the goal and challenge for cultural neuroscience is to identify the phenomena that can be readily mapped within and across multiple levels of analysis. There are at least three foreseeable benefits of a cultural neuroscience approach for basic and applied research: (1) merging the social and natural sciences, (2) informing interethnic ideology, and (3) enhancing the condition and care of human health across diverse cultural populations.

Merging the scientific study of culture and biology

The increasing stratification of the social and natural sciences within universities and academic subfields has led to deep conceptual and methodological schisms between different communities of researchers. In an influential lecture, Snow, an influential British physicist and novelist (1959), once famously characterized the fissure between social and natural sciences as ‘‘the two cultures.’’ Even within the field of anthropology, which Boas originally envisioned as simultaneously encompassing cultural and social anthropology, physical and biological anthropology, archaeology, and linguistics, there has historically been such deep intrafield antagonism, that some anthropology departments within the American universities have even split into two, with one-half of the department focused on cultural approaches, while the other half focused on biological approaches to the same questions (Shenk, 2006). Is the gap between cultural and biological sciences too wide to be bridged within a single discipline? How might consilience be achieved (Wilson, 1998)? Remarkably, anthropology is currently witnessing a rebirth of unification within its disparate branches through the emergence of neuroanthropology (Brown and Seligman, in press; Dominguez Duque et al., in press; Rilling, 2009; Seligman and Brown, in press). Akin to its sister field, psychology as a hub science (Cacioppo, 2007) stands in a natural position to merge the scientific study of culture and biology by harnessing theories and methods from every area of psychology, from evolutionary and cognitive to cultural and developmental. The empirical tools needed to investigate the links across multiple levels of analysis are available now in ways not previously imaginable. The cultural neuroscience framework represents an opportunity to transcend the confines of academic subfields and address age-old questions regarding the mutual constitution of cultural and biological influences on human behavior in novel ways.

Informing interethnic ideology

Research in cultural neuroscience may also inform public policy issues related to cultural diversity and interethnic justice. As a result of globalization, cultural communities of the world are becoming increasingly interdependent and interethnic, leading to an increasing urgency to understand how diverse communities of people may optimally coexist (Bodenhausen, in press;

Wolsko et al., 2000). On the one hand, interethnic ideologies such as colorblindness advocate treating people of different cultural heritages similarly, with no regard to interethnic differences. On the other hand, interethnic ideologies such as pluralism advocate embracing cultural differences and creating public policies that respect interethnic differences. Research in cultural neuroscience can potentially inform this important debate by studying how cultural identity affects the brain and behavior, whether or not cultural traits have adaptive value and how changes in cultural diversity may affect the human mind, brain, and behavior. At the same time, scientific rigor and ethical care is needed when seeking to apply cultural neuroscience evidence toward larger public policy discourse regarding how best to achieve optimal coexistence of diverse cultural and ethnic groups.

Implications for population health

Finally, the important interplay of culture and genes in the study of population health has long been acknowledged (Shields et al., 2005; Wang and Sue, 2005). For instance, whereas Ashkenazi Jews have a greater likelihood of Tay-Sachs disease, people from Northern Europe are more likely to develop cystic fibrosis (Exner et al., 2001; Wang and Sue, 2005). Another example of population differences in health as a function of differences in allelic frequency is the gene *CYP2A6* and nicotine addiction (Shields et al., 2005). Protective forms of the *CYP2A6* gene are very rare in Europeans and Africans (~3%), but more prevalent in Japanese and Koreans (~24%) (Shields et al., 2005). Cross-national epidemiological studies, including the 2008 World Health Organization cross-national survey of affective disorders, indicates significant variation in global prevalence of mental health disorders, such as anxiety and major depression (Kessler and Ustun, 2008; Weissman et al., 1996). How do differences in genetic frequencies affect brain systems and behavior underlying physical and mental health conditions? How do cultural factors influence the expression and function of these genes and their regulatory effects on brain and behavior?

The answers to these intriguing questions are finally within our empirical grasp. By using the cultural neuroscience framework to identify and investigate candidate phenomena using the multiple levels of analysis approach, we will enhance our chances of understanding how sociocultural and biological forces interact and shape each other as well as find potential ways to direct this knowledge toward timely issues in population health.

Cultural neuroscience as a once and future discipline

The beginning of the 20th century marked the formal birth of the study of culture, with the emergence of the field of anthropology and with cultural psychology joining forces with anthropology toward the latter half of the century. It is humbling to note that more than 100 years have since passed and scientists are still asking the same questions as Boas in 1907. Why does cultural diversity exist and what are its origins? Yet, it is encouraging to observe that the beginning of the 21st century marks the reunification of the study of culture and biology with the emergence of the field of cultural neuroscience. As challenges of living in an increasingly globalized and interethnic world increase, cultural neuroscience as a once and future discipline represents a necessary moment in the history of psychology and neuroscience, one that offers scientists with a fresh opportunity to transcend traditional academic confines and direct their intellectual prowess toward solving elusive, timeless questions on the nature and origins of human diversity. Whether or not it will take a century to pass before we gain a clearer grasp of how culture emerges from human biology and how human biology shapes culture remains to be seen.

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