

CHAPTER 9

Cultural Neuroscience

Parsing Universality and Diversity across Levels of Analysis

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The existence of human diversity has been a source of contemplation and curiosity since the beginning of human history. In his encyclopedia *Etymologiae*, published in the seventh century, Isidori of Seville observed that diversity among humans existed not only in their appearance, such as color or body size, but also in the content of their minds (Jahoda, 2002). Philosophers, such as Descartes and Locke, continued speculation on the nature and origin of human diversity, introducing more formalized notions of culture and its relation to human nature into the lexicon. The study of culture and its role in humanity gained further prominence with the emergence of the field of anthropology in the late 19th century, which emphasized the study of cultural variation through observation of the customs, practices, values, and beliefs of different cultural groups, and later with the field of cultural psychology, which sought to apply the methodology of psychology and its emphasis on the individual mind to the study of cultural variation.

Contemporary cultural psychologists have made considerable progress in documenting

cultural variation in human thought and action. The mutual constitution of culture and mind has been demonstrated in a variety of fundamental psychological processes, including the way people conceive of the self (Markus & Kitayama, 1991; Markus, Kitayama, & Heiman, 1996), how they make causal attributions (Morris & Peng, 1994), how they attend to and remember objects in their environment (Miyamoto & Kitayama, 2002; Kitayama, Duffy, Kawamura, & Larsen, 2003; Masuda & Nisbett, 2001), and how they perceive, experience, respond to, and predict their own and others' emotions (Elfenbein & Ambady, 2002; Lam, Buehler, McFarland, Ross, & Cheung, 2005; Mesquita & Frijda, 1992). A fundamental assumption of this research is that the human mind is intimately linked with its social world or cultural context, and that culture is continuously created through the actions and products of the individual minds that comprise it.

Cultural psychologists have been wary, however, about integrating biological perspectives into their research endeavors, perhaps because

they assume that investigations into the biological bases of the mind reflect an empirical search for human universals rather than cultural differences (Norenzayan & Heine, 2005; Smedley & Smedley, 2005). Likewise, cognitive neuroscientists have viewed their discipline as a pursuit of universal truths rather than culturally specified instances about how the brain gives rise to the mind and vice versa (Kosslyn, 1999). Yet a growing number of studies show that both the structure and the function of the developing human brain is shaped both by the environment and by cultural experiences (Johnson & Munakata, 2005). Moreover, although recent advances in human genomics and molecular biology demonstrate that whereas the majority of the human genome is conserved across human cultures, variation in the frequency of different genes does exist between different human populations. This variation of genes between cultures suggests that cultural variation may emerge at multiple levels, possibly as a result of interactions between levels (e.g., gene–brain, culture–behavior, culture–gene, culture–brain–gene; Bonham, Warshauer-Baker, & Collins, 2005). Thus, we argue that cultural psychologists' notions of the "mutual constitution" of culture and mind needs to be broadened beyond interactions between culture and the mind, to interactions among culture, genes, and the brain.

Early articulations of this idea of bidirectional influences among culture, genes, mind, and the brain can be traced to the work of prominent developmental psychologists such as D'Arcy Thompson and C. Waddington, who laid down the original framework for what would later come to be known as *probabilistic epigenesis* (Johnson, 1997). According to this view, humans come into the world with sets of possible developmental trajectories (each with their own alternative end states, presumably described by the genome) that are then pursued, or not, over the course of development as a result of interactions with environmental input. The notion of *biocultural co-constructivism* was introduced more recently to account for the significance of plasticity across development in gene–environment interactions; humans may come into the world with a set of possible developmental trajectories, but once on a certain trajectory, plasticity may alter both the path and the end state (Li, 2003, Chapter 21, this volume). The empirical challenge brought on by both views is finding ways

to articulate precisely how neural mechanisms and psychological capacities emerge through complex, multilevel interactions between genetic forces and the cultural environment.

To designate an approach to meet this challenge, we introduce in this chapter the term "cultural neuroscience," which is a theoretical and empirical approach to investigate and characterize the mechanisms by which this hypothesized bidirectional, mutual constitution of culture, brain, and genes occurs. Specifically, we suggest that biological factors may lead to cultural variation at the neural and genetic levels, and that cultural factors may lead to variation in brain structure and function, as well as gene expression. To accomplish this, we first focus on identifying the conceptual landscape covered by the term "cultural neuroscience." Second, we describe the methodological tool box needed for accomplishing cultural neuroscience research. Third, we review recent progress in identifying cultural variation at the genetic and neural levels. Fourth, we discuss the nature and meaning of cultural variation across different levels of analyses. Finally, we identify important challenges and considerations that need to be addressed for cultural neuroscience to progress systematically and significantly.

CULTURAL NEUROSCIENCE: DEFINING THE LANDSCAPE

Cultural neuroscience is an area of research that investigates cultural variation in psychological, neural, and genomic processes as a means of articulating the interrelationship of these processes and their emergent properties (see Figure 9.1). A multilevel analytic approach to studying psychological phenomena and human behavior has become more popular, as demonstrated by the number of subfields that have proliferated in recent years, each incorporating neuroscience into a parent social science discipline; these include social neuroscience (Cacioppo, Lorig, Nusbaum, & Berntson, 2004), social-cognitive neuroscience (Ochsner & Lieberman, 2001), affective neuroscience (Davidson, 2003), and neuroeconomics (McCabe, 2003). Whereas cultural neuroscience shares the goal of these subfields to explain a given phenomenon in terms of an emergent property of interactions between mental and neural events, cultural neuroscience is distinctive in that it focuses squarely on examin-

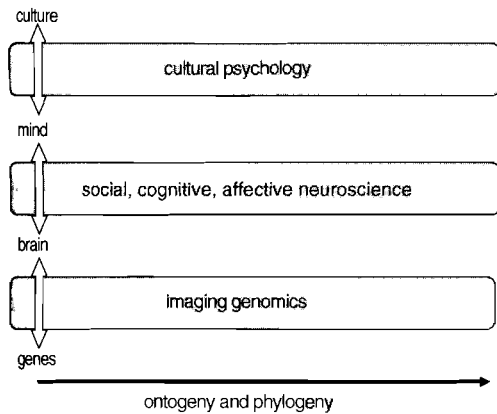


FIGURE 9.1. Diagram of the cultural neuroscience framework.

ing psychological and neural processes that may vary across cultural groups in some meaningful way. Cultural neuroscience can be seen as a complementary endeavor to evolutionary psychology (see review by Cosmides, Tooby, & Barkow, 1992); however, whereas evolutionary psychology seeks to articulate the universal, evolved architecture of the mind shared by all humans, cultural neuroscience emphasizes cultural variation, specifically, investigating interactions between events at the psychological, neural, and genetic levels.

The Neuroscience of Culture versus Race

The goals and research questions of cultural neuroscience are to a certain extent similar to those driving the modern neuroscientific study of race. In recent years, the importance of social experience on brain function has been highlighted by studies showing that racial group membership affects neural processes underlying other basic aspects of social cognition, such as face perception and recognition, as well as social evaluation and bias (see Eberhardt, 2005, for a review). Work in this area has been groundbreaking in demonstrating how racial group membership (and racial experience more generally) can modulate the neural activity underlying basic perceptual and cognitive processes. Cultural neuroscience, however, is likely to illuminate how sociocultural and biological factors influence each other in ways not previously revealed by neuroscientific studies of race. Culture and race differ in a number of important respects (Betancourt & Lopez, 1993).

Culture refers to shared meaning systems, social practices, geographical space, social and religious values, language, ways of relating, diet, and ecology (Markus et al., 1996). In contrast, the concept of race, which typically refers to physical characteristics such as skin color, facial features, and hair type shared by people of a given ancestral origin, is shrouded in controversy about whether “race” refers solely to biological or socially constructed features that differentiate groups of people (Bonham et al., 2005; Smedley & Smedley, 2005). Individuals may belong to different races but may share the same culture. Whites, blacks, Hispanics, and Asians living in America, for example, share the same government structure and, to some extent, the same language, ecology, social values, and ways of relating, but are considered members of different racial groups. When neuroscience investigations of race and brain function include participants from the same culture (which, to date, all studies have), they do not capture how different meaning systems (e.g., collectivism and individualism), languages (e.g., Chinese and English), ways of reasoning (e.g., dialectism), and so on, may arise from, as well as alter, neural processing and genomic expression.

The suggestion that broad phenomena such as culture can be understood in terms of interactions between multilevel events (e.g., neural, situational, genetic) may be construed as a form of reductionism and may therefore be subject to criticisms typically associated with reductionist agendas. Philosophers of science and scientists of all kinds have long grappled with the problem of whether complex phenomena, such as consciousness, are truly reducible to their component parts (Dennett, 1995; Nagel, 1998). For instance, does reducing the phenomenon of consciousness into a description of neural events somehow fail to capture the context within which consciousness occurs, and do the phenomena that emerge from these neural events differ from the actual events themselves? The aim of cultural neuroscience is *not* to “reduce” culture into a description of genetic and neural processes at the expense of the characterization of emergent properties, nor is it intended to replace the language of culture with the language of neurons or molecules. The goal of a cultural neuroscience approach is empirically to shed light on the extent to which the cultural variation observable in human behavior and mental life is traceable to cultural

variation at other levels of analysis and their interaction, including the biological and neural levels.

THE CULTURAL NEUROSCIENCE TOOL BOX: INTEGRATING METHODOLOGIES

What makes the study of cultural neuroscience a more viable empirical and theoretical proposition for modern scientists is the amalgamation of recent methodological advances in the fields of cultural psychology, cognitive neuroscience, and molecular biology. In recent years, cultural psychologists have made significant advances in articulating the criteria for creating culturally appropriate behavioral measures that ensure the psychological phenomenon of interest is testable in people of all cultures (Norenzayan & Heine, 2005). Cognitive neuroscience has revolutionized the study of the mind and brain by developing an arsenal of techniques for mapping neural structures to psychological functions at varying degrees of spatial and temporal resolution (Gazzaniga, Ivry, & Mangun, 2002; Handy, 2005; Heeger & Ress, 2002). Molecular biology has seen rapid transformation in recent years with the development of tools for enabling the efficient and economical translation of the human genome (Hariri & Weinberger, 2003). Taken together, the convergence of these tools enables the unprecedented ability to investigate the mutual constitution of genes, brain, behavior, mind, and culture (see Figure 9.2).

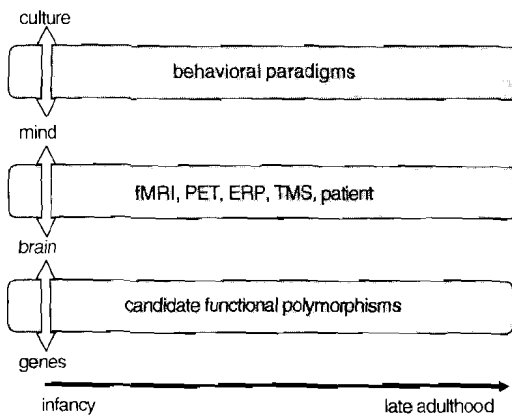


FIGURE 9.2. Diagram of the cultural neuroscience tool box.

Behavioral Paradigms

The first important tool in the cultural neuroscience tool box is a compilation of *behavioral paradigms* appropriate for examining cognitive, perceptual, emotional, and social-cognitive phenomena in people of different cultures. The development of cross-culturally sensitive behavioral paradigms has proved challenging in several regards. The ways that tasks are created and administered may favor one cultural group over another in ease and intuitiveness; specifically, cultural differences may exist in response styles where people of certain cultures are more comfortable with completing questionnaires relative to others (Greenfield, 1997). Participants of certain cultures may be more likely to use the center rather than the extremities of a scale in a questionnaire (Chen, Lee, & Stevenson, 1995). Free-response formats requiring extensive translation may produce errors in meaning; such errors may also arise when translating the instructions of measures from one language to another (Brislin, 1970). Responses associated with demand characteristics may be more frequent when sampling from cultures that value "saving face" above accurate self-report (Heine, Takata, & Lehman, 2000), and culture may affect the different social referents used when providing self-reports (Heine, Lehman, Peng, & Greenholtz, 2002). Psychologists have created a number of solutions to these methodological worries, including back-translation (Brislin, 1970), incorporating different kinds of behavioral measures in a study (Nisbett & Cohen, 1996), and even using hidden behavioral measures (Heine et al., 2000).

Convergent Neuroscience Methods

The second component of the cultural neuroscience tool box is *convergent neuroscientific methods* for characterizing the neural processes underlying a given psychological function. There are several neuroscience tools available to psychologists interested in mapping neural structure to mental function, including functional MRI (fMRI), positron emission topography (PET), transcranial magnetic stimulation (TMS), magnetoencephalography (MEG), and event-related potentials (ERPs); each tool has its strengths and weaknesses (Gazzaniga et al., 2002). Imaging techniques, for example, such as fMRI and PET have very good spatial reso-

lution (in cubic millimeters) and are crucial to identifying which brain regions are involved in different aspects of processing (Heeger & Ress, 2002). However, because they record differences in blood flow, which occurs on the level of seconds, and not neural activity directly, which occurs on the level of milliseconds, imaging techniques lack temporal precision. Cortical recording techniques, such as the ERP, are extremely temporally precise, because they directly record neural activity to the precision of milliseconds and are therefore good for determining when a process is occurring or when a difference in neural processing emerges (Handy, 2005). Unlike fMRI and PET, the ERP lacks spatial precision, because it records electrical signals only from cortical regions directly under the scalp. This is particularly problematic for the study of subcortical areas, such as the amygdala, that have been strongly implicated in the processing of emotions. MEG, a methodology with both the advantages of brain imaging techniques and ERPs directly records electrical activity from the brain, thus having extremely high temporal resolution. MEG also has good spatial resolution due to the high number (e.g., approximately 300 channels) and sensitivity of the channels used to record electrical activity.

TMS and studies of patients with brain lesions are currently the only way of discerning which regions in a normal brain are *necessary* for performing a certain function, such as recognizing faces or emotional expressions. TMS uses rapidly changing magnetic fields to induce electric fields in a specific brain region and can be applied repetitively (Paulus, Hallett, Rossini, & Rothwell, 1999). In a typical TMS experiment, a powerful magnet that is held over a cortical region of the brain (e.g., the motor cortex or frontal gyri) delivers magnetic pulses for a few minutes. The application of these magnetic pulses affects electrical and biochemical activity in the directed brain region and in interconnected brain regions. Typically, the region in which TMS is applied undergoes suppression of activity or temporary dysfunction, creating a "temporary functional lesion." If this neural dysfunction is accompanied by behavioral decline, one can infer that a given brain region is *necessary* for a particular mental function. Similarly, by testing a given behavioral paradigm in patients with discrete brain lesions, one can infer whether or not a brain region is *necessary* to produce a certain behavior.

Disadvantages of patient studies are that lesion sites rarely completely overlap nor is severity of brain damage identical across patients. Such heterogeneity in location and severity of brain lesions may affect the degree to which one can infer that a specific area of the brain is critical. Thus, the advantage of TMS is that one can examine the necessity of a given neural structure within the same location across several normal brains.

Given their different strengths and weaknesses, no individual neuroscientific method can independently capture the rich complexity with which the brain processes cognitive and emotional information. Rather, it is the convergence of findings from multiple techniques that enables us to make sound inferences about neural structures and their psychological function. ERPs tell us when neural processes are occurring. MRI and fMRI provide information about the structure and function of the human brain. TMS and patient populations provide information about whether a given brain region is necessary for a given psychological function.

Genes and Their Functional Polymorphisms

Genes, the fundamental physical and functional unit of heredity, substantially influence every level of human biology, including neural function and mental processes. Genes are thought to account for a majority of psychiatric illnesses, prompting many studies that attempt to map specific genes onto various cognitive, emotional, and personality styles and disorders (Hariri & Weinberger, 2003). The entire human genome comprises a relatively small number of unique genes, approximately 20,000 to 30,000, many of which are found in the genomes of other species, from simple organisms, such as bacteria and fruit flies, to more complex ones, such as sheep and monkeys (Cavalli-Sforza, 2005). Although the actual number of genes is small, individual genes can take on various forms, known as polymorphisms, that result from evolutionary "mistakes" whereby the original genetic structure is modified in small but significant ways: through snips, repeats, and deletions of base pairs. There are approximately 3 million polymorphic variation sites in the human genome, and it is the variation in these sites across populations and subpopulations that has yielded surprising and potent insights into the possible origins of psychological and neural differences

across individuals and cultures (Cavalli-Sforza, 1998, 2005).

Hence, the third part of the cultural neuroscience tool box is a means of determining the presence or absence of functional polymorphisms and their variants in an individual. Identifying functional polymorphisms is important to designing experiments that test whether a given neural or mental process is influenced by one's genome. Blood samples and cheek swabs are the primary ways of obtaining DNA from individuals; body samples are then amplified through polymerase chain reactions (PCRs) tailored to isolate specific functional polymorphisms (Gelernter, Kranzler, & Cubells, 1997). Once the variants of a given polymorphism in an individual is identified (e.g., short or long allele carrier), they can then be separated into different groups and the participant's neural and psychological responses can be compared in light of his or her genomic profile.

These three basic components of the cultural neuroscience tool box—(1) culturally appropriate behavioral paradigms, (2) neuroscience tools, and (3) functional polymorphisms—offer an unprecedented amount of experimental power for cross-level analyses of cultural variation. These tools allow the measurement of individual mental, neural, and genomic information, and comparisons of individuals from different cultures at every level. A multilevel analysis has long been considered necessary for a full articulation of the mutual constitution of culture and the mind; the unification of novel experimental techniques in the cultural neuroscience tool box described earlier provides the means to achieve this. As existing tools improve and new tools are introduced, the tool box will need to be updated and refined.

CULTURAL VARIATION IN BEHAVIOR

Numerous behavioral studies, mostly comparing Easterners (e.g., Chinese, Japanese) and Westerners (e.g., Western Europeans, European Americans), suggest that there is significant cultural variation in basic psychological processes, including mathematical thinking, reasoning style, memory, emotion, and the self (see review, in Markus & Kitayama, 1991; Nisbett & Norenzayan, 2002). For example, Mandarin speakers talk about time as if it were vertical,

whereas English speakers refer to it as horizontal (Boroditsky, 2001). Easterners tend to attend to the background or situation, whereas Westerners focus on the object within a scene (Masuda & Nisbett, 2001). Furthermore, Easterners tend to perceive objects and people, and the situation in which they are embedded as mutually interdependent; thus, they may use holistic strategies for perceiving people and scenes. Westerners, however, who are more likely to perceive objects and people as independent from the situation, apply a more analytic strategy for perceiving entities in their environment (Nisbett & Norenzayan, 2002). These examples provide a window into the degree to which culture shapes basic psychological processing and serve as a foundation for research that examines cultural variation at other levels of analysis, including genes and the brain. Because behavioral findings that document cultural variation in mind and behavior are well represented in other chapters, we focus our discussion on cultural variation beyond behavior.

CULTURAL VARIATION IN THE BRAIN

The vast majority of cognitive neuroscience research has focused on elucidating functional relationships among brain, mind, and behavior, which are presumed invariant across cultures (Plomin & Kosslyn, 2001). However, there are several reasons to suspect meaningful cultural variation in brain structure and function. First, as discussed earlier, there seems to be significant cultural variation in functional polymorphisms associated with primary cognitive and affective capacities. Furthermore, approximately 70% of genes are expressed in the brain. Thus, cultural variation in brain function is possible to the extent that these functional polymorphisms affect efficiency and capacity of neurotransmission (Hariri & Weinberger, 2003). Second, experience, particularly perceptual or social experience during certain periods of development, can play a definitive and shaping role in the acquisition and maturation of neural mechanisms underlying a wide range of fundamental skills, including language (Neville & Bavelier, 1998), music comprehension (Janata & Grafton, 2003), face processing (Gauthier & Nelson, 2001), and spatial navigation (Wolbers, Weiller, & Buchel,

2004; Maguire et al., 2000). To the extent that cultural rules, values, beliefs, and practices shape perceptual and social experience, and to the extent that experience differs between cultures, cultural differences in neural responses underlying cognitive and affective processes are likely to exist (Park & Gutchess, 2002). Third, behavioral research suggests significant cultural variation, particularly between Westerners and East Asians, in their basic perceptual, cognitive, and affective strategies, that may have emerged as a result of divergent philosophical and reasoning traditions (e.g., holistic vs. analytic) between the East and West (Nisbett, Peng, Choi, & Norenzayan, 2001). To the extent that neural mechanisms underlie psychological ones, we would expect to find differences in neural activity for psychological functions where notable behavioral differences exist between cultures. Finally, the neural bases of a given mental function may vary across cultural groups either in terms of structures and circuitry recruited to perform a given task (e.g., to recognize emotions or colors) or the degree to which these structures are activated during the task, even in absence of observable behavioral or genetic differences. Thus, investigating cultural variation in brain structure and function is both a viable and necessary endeavor for fulfilling the goals of both cultural psychology (e.g., to articulate meaningful cultural differences) and cognitive neuroscience (e.g., to identify and explain brain structure and function).

Despite notable progress in describing cultural variation at the behavioral and genetic levels in recent years, still relatively little is known about the ways the structure and function of the human brain vary across different cultures. To date, the lion's share of empirical research on cross-cultural differences in the brain has been in the domain of language (e.g., the neural bases for cross-linguistic differences and multilingualism; Paulesu et al., 2000; Bolger, Perfetti, & Schneider, 2005; Xue, Chen, Jun, & Dong, 2006). Empirical progress in investigation of cross-cultural differences in neural activity for a broader range of psychological phenomena, from object perception (Ketay, Hedden, Aron, Markus, & Gabrieli, 2005) and theory of mind (Kobayashi & Temple, 2004) to music (Morrison, Demorest, Aylward, Cramer, & Maravilla, 2003) and taste perception (McClure et al., 2004), is also growing rapidly.

CULTURAL VARIATION IN THE HUMAN GENOME

Incredible controversy has ensued in recent years over the question of whether racial or cultural differences exist at the level of the human genome and if it even makes sense to apply concepts such as race and culture to the genome (Sankar & Cho, 2002; Wang & Sue, 2005). Such controversy is not without merits. The human genome is incredibly conserved, with only approximately 0.2% to 0.4% of the genome varying across individuals (Tishkoff & Kidd, 2004). Mutation, migration, genetic drift, and selection are all sources of normal genetic variation in cultures (Cavalli-Sforza, 1998, 2005). Individual genomic variation accounts for approximately 90% of total genomic variation. There also exists variation in genes at the population level, but on a much smaller scale, because people are more likely to mate with others who live close to them, and to share the same language and phenotypic qualities (e.g., assortative mating; Tishkoff & Kidd, 2004; Wang & Sue, 2005). Given that the majority of the genome does not appear to vary across cultural groups or populations, does it even make sense to pay attention to cultural variation in genomic frequencies?

We argue that although it occurs on a much smaller scale relative to individual genetic variation, genomic variation at the population level should not be ignored; instead, it should be considered seriously, with scientific rigor and ethical care. We prefer to discuss population variation in the genome in terms of culture rather than race, because culture refers not only to ethnic heritages and phenotypic similarities between individuals but, perhaps more importantly, also to shared lifestyles, diet, geographical region, and other environmental aspects that likely have a significant interaction with brain function, gene expression, and selection. Both the sheer range of genomic frequency variation in the number of genes that demonstrate group frequency variation and the number of cultural groups for which frequency distribution differs are impressive, posing a formidable challenge for molecular biology research (Cheung et al., 2000). Indeed, molecular biologists have designed online databases (e.g., ALFRED¹) on the Web to facilitate public dissemination of catalogues documenting variation in genomic frequencies for populations all over the world: from the Khung San tribe in Af-

rica to the Yemenites in Eastern Europe (Osier et al., 2002). Although it is possible that cultural variation in allelic frequency for many genes will not have direct functional consequences on the mind or brain, there is growing evidence to the contrary. Here, we highlight two functional polymorphisms, *DRD4* and *5-HTT*, with significant cultural variation in genomic frequencies that has already been demonstrated to influence psychological and neural mechanism substantially.

***DRD4*: Dopamine Regulator Gene**

The dopamine receptor gene, *DRD4*, is one of the most polymorphic genes. Variants of the *DRD4* vary in the number of imperfect 48 base pair (bp) tandem repeats, ranging from 2 to 11 repeat units, but most commonly 4 to 7 repeats. The number of repeat units on the *DRD4* affects the size of the dopamine receptor and its ability to bind to dopamine-like molecules (Benjamin et al., 1996). Variation of the *DRD4* gene has been linked to novelty-seeking behavior and psychiatric disorders (Gelernter, Kranzler, Coccaro, et al., 1997). Considerable evidence suggests that the seven-repeat *DRD4* variant is involved with increased novelty-seeking, risk-taking behavior and hyperactivity (see review by Munafo et al., 2003). The frequency of long versus short-allele carriers of the *DRD4* gene varies significantly across cultures. A low proportion of the East Asian population carries the long-allele variant of *DRD4* (e.g., 1% carry seven repeats), whereas an extremely high proportion of the South American Indian population carries the long-allele version (e.g., 78% carry seven repeats; Chen, Burton, Greenberger, & Dmitrieva, 1999).

There are several possible explanations for this cultural variation in the genome. One is the *founder's effect*, whereby a higher proportion of long alleles within a migratory population may be due to the fact that founders of that population migrated as a behavioral consequence of carrying the long allele of the *DRD4*, which promoted exploratory behavior. A second possibility is *natural selection*, whereby South Americans carrying the long allele had an advantage relative to their short-allele-carrying counterparts, thus providing them with a reproductive/survival advantage. A third hypothesis is *random mutation*, whereby frequency differences in long- versus short-allele versions of *DRD4* within a small population

result from spontaneous mutation, such that over each successive generation, by chance, long-allele individuals leave more descendants relative to short-allele individuals, which then leads to a reduction in heterogeneous genetic variation within that population over time.

Chen and colleagues (1999) conducted regression analyses to determine the factor(s) driving the variation of *DRD4* between East Asians and South American Indians. In particular, they compiled existing data on *DRD4* allele frequencies of 2,320 individuals from 39 populations, and on the long-term migration pattern (e.g., 1,000 to 30,000 years ago) for these populations. They found that populations known to migrate had a significantly larger proportion of individuals with the long allele of the *DRD4* relative to nonmigratory populations. Chen and colleagues speculate that this association is not due to founder's effects, because the rate of long alleles of *DRD4* is identical for immigrants (e.g., Chinese and Japanese immigrants in the United States) and their respective comparison group (e.g., Chinese in China and Japanese in Japan). This suggests that the increased rate of long alleles among migratory groups more likely resulted from adaptation to the challenges of migration rather than to a particular subset of individuals who founded the migratory groups. Future research is needed to determine whether the striking cultural variation in *DRD4* allele frequency between East Asian and South American populations corresponds with cultural variation in neural mechanisms underlying novelty-seeking behavior, risk taking, or hyperactivity.

***5-HTT*: Serotonin Regulator Gene**

The serotonergic uptake transporter gene, *5-HTT*, is another polymorphism known for cultural variation. *5-HTT* codes for proteins that regulate the reuptake of serotonin at brain synapses and plays a critical role in the regulation of emotional processes. Similar to variants of the *DRD4* gene that differ in length, the two main variants of the *5-HTT* gene, short (*s/s*) and long (*l/l*), differ in the length of the promoter region that subsequently affects when, where, and how much protein is made. The long allele of the *5-HTT* is associated with higher transcription efficiency relative to the short allele, ultimately promoting higher levels of serotonin in the synapse.

Behavioral genetics studies examining the functional role of *5-HTT* in emotion have found that individuals carrying the short allele were slightly more prone to abnormal levels of anxiety relative to long-allele carriers (Lesch et al., 1996), a finding later corroborated by others (Katsuragi et al., 1999; see review by Sen, Burmeister, & Ghosh, 2004). People with the short allele were also found to acquire conditioned fear responses more readily than those without this allele (Garpenstrand, Annas, Ekblom, Orelund, & Fredrikson, 2001). Finally, a study by Caspi and colleagues (2003) showed that individuals with the short allele for this gene were more susceptible to stressful life events and twice as likely to suffer from depressive symptoms, diagnosable depression, and suicidality compared to individuals with the long allele.

Further evidence for a critical role of *5-HTT* in emotion processing comes from imaging genomics research examining the relationship between *5-HTT* and brain function. In particular, recent work has linked the *5-HTT* serotonin uptake gene to amygdalar function. A recent imaging genomics study by Hariri and colleagues (2002) demonstrated that individuals with the short allele showed greater amygdalar activation during an emotion-matching task relative to individuals with the long allele. Another imaging study by Furmark and colleagues (2004) found enhanced right amygdalar response in social phobics with one or two copies of the short allele compared to social phobics who were homozygous for the long allele during anxiety provocation. Greater amygdalar reactivity in response to emotional stimuli in short-allele carriers relative to long-allele carriers may underlie their heightened sensitivity or arousal to emotional stimuli, ultimately leading to higher rates of anxiety and depression disorders. These findings, though preliminary, are groundbreaking, because they show a direct relationship between genes and brain function, whereas previously researchers had only been able to study the relationship between genes and behavior. Moreover, examining the link between genes and brain function may prove more fruitful than studying the link between genes and behavior, because genetic variation in both studies accounted for more than 20% of variance in brain function even though no differences in behavioral measures (e.g., emotion matching task) emerged between the short- and long-allele groups in these particular studies.

Critically, Japanese and Caucasians from Western Europe and the United States significantly differ in the number of individuals within the cultural group that carry the short versus long allele of the *5-HTT* genotype. Several behavioral genetics studies have reported that in a typical Japanese sample, 70–80% of individuals carry the short allele (s/s or s/l) compared to 20–30% of individuals carrying the long allele. In a typical Caucasian sample, 55–60% of individuals carry the long allele and only 40–45% of individuals are short-allele carriers of the *5-HTT* genotype (Gelernter, Kranzler, & Cubells, 1997; Gelernter, Kranzler, Coccaro, et al., 1997; Hariri & Weinberger, 2003). Several behavioral genetics research groups have also reported this cultural difference among independent samples of Japanese and Caucasians, further validating this potentially important finding (Kumakiri et al., 1999). A critical research direction for the future is to investigate the relationship between this cultural difference in frequency of short-versus long-allele carriers of *5-HTT* and cultural differences in behavioral performance on anxiety, personality or emotion measures, as well as brain functioning, such as in amygdalar reactivity to emotional stimuli (Chiao et al., 2004).

To the extent that *5-HTT* is relevant to normal and abnormal emotion processing, it is important to consider how and why Japanese and European populations differ so dramatically in their ratio of short- versus long-allele carriers and what implications this has for cultural differences in emotion at the neural and behavioral level.² Behavioral geneticists speculate that the population differences may reflect a combination of varying behavioral adaptation in different populations, adaptation related to other phenotypes, and genetic drift of another important but neutral polymorphism (Gelernter, Kranzler, & Cubells, 1997; Gelernter, Kranzler, Coccaro, Siever, & New, 1998). Whether this difference in frequency of short- versus long-allele carriers between Japanese and Caucasian populations drives the cultural variation in cognition and emotion observed at behavioral and neural levels is an intriguing question for future research.

Despite growing evidence that substantial variation in genomic frequencies exists across cultures, we are only beginning to understand its functional scope and the broader implications for explaining cultural variation in psy-

chological processes, brain structure, and function. Enthusiasm for this endeavor is to be met with caution, because scholars need not look too far back in history for examples of arguments whereby genomic differences across the races were documented as a means of justifying a racial hierarchy (Eberhardt, 2005; Fraser, 1995). As Gould (1981) and others have aptly cautioned, science does not operate solely in an objective vacuum but in the mosh pit of social, political, and historical ideologies and environments. Scientists should be aware of the moral issues at stake when conducting cultural neuroscience research and take responsibility to protect against potential misuse or misinterpretation of their findings by the lay public, media or naïve scholars.

Correspondence of Culture Variation across Levels of Analysis

One way that investigations of cultural differences in brain function may prove useful is to provide converging evidence that extends behavioral research to demonstrate cultural differences in cognitive, emotional, or perceptual abilities. A recent fMRI study comparing neural activity during the Framed Line Test (FLT) between East Asians living in the United States for less than 7 years and European Americans provides a compelling example (Ketay et al., 2005). Originally created by Kitayama and colleagues (2003), the FLT assesses one's capacity both to incorporate and to ignore contextual information in a nonsocial domain. In the original version of the FLT, participants are presented with a square frame with a vertical line embedded within it and are then shown another square frame of the same or different size. They are asked to draw a line that is either identical to the first line in the first square frame in absolute length (absolute condition) or proportionate to the height of the surrounding frame (relative condition). The absolute condition requires one to ignore the context (both the first and second frame) when reproducing the line, whereas the relative condition requires one to incorporate context when reproducing the line. Results from a previous behavioral study of the FLT showed that Asians were more accurate in the relative condition, whereas European Americans were more accurate in the absolute condition (Kitayama et al., 2003).

In the recent neuroimaging study of the FLT, participants performing a modified version of

the task viewed a series of stimuli, each comprising a line inside a square, both of which varied systematically in size across trials. Specifically, participants judged whether either (1) the proportional size of the line relative to the square was the same as the stimuli just seen in the previous trial (relative condition) or (2) the absolute length of the line, regardless of the square size, was the same (absolute condition). Results from this study revealed cultural variation in neural responses to the extent that certain brain regions were recruited to perform the relative and absolute line judgment tasks. East Asians demonstrated greater recruitment of the dorsolateral prefrontal cortex (DLPFC), a brain region important in working memory tasks, for absolute versus relative line judgments, whereas European Americans showed more engagement of the anterior cingulate cortex (ACC), a brain region typically engaged during cognitive conflict, for relative versus absolute line judgments. These fMRI results extend previous behavioral results showing that East Asians and European Americans use different cognitive strategies to perceive objects embedded within a background by demonstrating differential recruitment of neural circuitry during such perceptual judgments between cultural groups.

Culture Variation in Neural Systems

Cultural differences may also exist at the neural level, even in the absence of cultural differences in the behavioral level. For example, an fMRI study by Gutchess, Welsh, Boduroglu, and Park (2006) compared neural activation between East Asian Americans and European Americans as they performed unintentional encoding of a series of pictures of objects (e.g., elephant), backgrounds (e.g., beach) and objects embedded in meaningful backgrounds (e.g., elephant on a beach), and rated how pleasant they found the pictures (e.g., *pleasant*, *neutral*, or *unpleasant*). After scanning, participants were given a surprise recognition test. Ratings of pleasantness did not interact with the culture of participants. Moreover, East Asian Americans and European Americans performed equally well, suggesting that task difficulty was equivalent across the two groups of participants, but significant group differences emerged in recruitment of distinct brain regions. Specifically, European Americans activated more regions implicated in object pro-

cessing, including the bilateral middle temporal gyrus, left superior parietal/angular gyrus, and right superior temporal/supramarginal gyrus. These results suggest that people of different cultural groups may use different encoding strategies and recruit different neural systems, even though both groups perform on object recognition tasks with equivalent behavioral competence.

In a cross-cultural fMRI study conducted in our laboratory on the neural bases of emotion recognition, Japanese participants, living in Japan, and European American participants, living in the United States, were scanned while explicitly recognizing Japanese and European American happy, neutral, fearful, and angry facial expressions (Chiao et al., 2004). Behavioral results indicated that all participants recognized facial expressions in Japanese and European American faces equally well. However, neuroimaging results showed that more Japanese than European American participants recruited distinct neural networks while judging ingroup versus outgroup emotional expressions. Hence, cultural variation in how the brain processes information may exist even when cultural variation is not observable in behavior; thus, inquiry into cultural variation at the neural level has the serious potential to provide novel insight into the universality and cultural specificity of neural processing.

Culture as Experience

Another way that cultural differences at the neural level may emerge is in brain regions that are experience-dependent or experience-sensitive. Modulation in these regions reflects the degree of familiarity or exposure to a given type of stimulus or task and may be accompanied by heightened skill or proficiency in a given behavioral task. One example of this kind of cultural difference at the neural level comes from fMRI and ERP face recognition studies in adults, showing that activity in the fusiform gyrus differs for faces of different racial or cultural groups and may be moderated by degree of interracial exposure (Golby, Gabrieli, Chiao, & Eberhardt, 2001). Another example of the influence of musical expertise or familiarity on neural responses comes from studies comparing neural responses to music in professional musicians and in novices. Recent ERP research suggests that familiarity with a given musical instrument alters neural re-

sponses to that instrument's sound. In particular, Turkish listeners showed a greater P3 amplitude response to hearing music from a familiar instrument (e.g., *ney*) relative to an unfamiliar instrument (e.g., cello), suggesting that hearing familiar music increases the allocation of attentional resources during memory (Arikan et al., 1999). Moreover, Morrison and colleagues (2003) used fMRI to compare neural activity in professional musicians (expert) and novices (control) while they listened to music of their own (Western-familiar) versus other culture (Chinese-unfamiliar). They found no difference in neural responses during listening to Western versus Chinese music in either music experts or novices, supporting the view that differences in cultural content (e.g., genre of music) do not necessarily affect brain responses. However, professional musicians demonstrated greater activity in the right superior temporal gyrus in response to both music genres, and in the right midfrontal region for Western music and the left midfrontal region for Chinese music. This latter finding indicates that expertise or training in a given skill, namely, listening to music, enhances activity in brain regions underlying that capacity. Moreover, the rostromedial prefrontal cortex in Western music experts demonstrates sensitivity to Western tonal structure, such that different voxels within this region activate for different tonal keys (Janata et al., 2002). Taken together, these studies illustrate how cortical responses may be shaped by cultural experience.

Culture as a Perceptual Filter

Culture may influence cortical responses not only through the shaping of perceptual experience but also by providing a body of semantic knowledge with which to filter and interpret perceptual experiences. In an interesting attempt to examine whether cultural knowledge influences perceptual experience and its neural correlates, McClure and colleagues (2004) compared neural activity while drinking either Coke or Pepsi. Double-blind behavioral tests indicated that people demonstrate strong preferences for either Coke or Pepsi. Moreover, regression analyses comparing behavioral and neural data revealed that activity in the ventromedial prefrontal cortex (VMPFC) was positively correlated with these behavioral preferences for anonymously delivered Coke and Pepsi. Moreover, when delivery of Coke or

Pepsi was preceded by cultural information (e.g., picture of a Coke or Pepsi can), a broader range of brain regions was recruited, including bilateral hippocampus and DLPFC, relative to when delivery was preceded by a simple light. These results suggest that taste preferences are shaped by at least two kinds of neural response: (1) in the VMPFC, associated primarily with the chemical composition of the drink; and (2) in the bilateral hippocampus and DLPFC, associated with cultural knowledge of the drink. Thus, cultural associations to drinks built up over time through exposure to advertisements, can influence neural activity during gustatory perception and significantly shape gustatory preferences.

FURTHER METHODOLOGICAL CONSIDERATIONS FOR CULTURAL NEUROSCIENCE RESEARCH

The growing number of cultural neuroscience investigations demonstrates the viability of a cultural neuroscience approach. However, just as early cross-cultural behavioral research was hampered by methodological problems, it is important to address methodological issues that hinder the progress of cultural neuroscience research on questions of interest.

Inclusion of Participants from All Cultures

The first issue involves participant sampling and access to necessary equipment. Currently, neuroscience research is conducted on expensive, stationary, and high-maintenance equipment (e.g., fMRI, ERP) available predominantly in rich, industrialized regions within North America, Japan, and Western Europe. Successful application of neuroscience methods to psychology questions requires extensive user training and technical support. This situation severely limits this research to these geographical regions or countries, therefore limiting the groups of participants studied. Evidence of a sampling bias is evident, because over 96% of imaging sites where basic cognitive and affective neuroimaging research is conducted are based in Western Europe or the United States (Raichle, 2003). Thus, one methodological problem that needs to be resolved is how to facilitate neuroscience research for scientists and participants in cultures where the technology and scientific instrumentation necessary to conduct these experiments is absent or difficult

to access. A possible solution is to develop and use neuroscience methods that are transportable to countries where the cultural group of interest resides. The solution to the problem of how to facilitate neuroscience research in regions of the world where the necessary technology does not exist or is difficult to access is likely to require international cooperation and support from governments and private institutions in countries where the necessary scientific technology and infrastructure is already available. Although this is a challenging problem, finding ways to include diverse populations in neuroscience research is crucial to characterize fully mechanisms and structures in the human brain.

Testing within a Culture or between Cultures?

To sidestep this participant sampling problem, most cross-cultural neuroscience investigations to date have been conducted at one scanner site, using recent immigrants or bilingual speakers as participants, rather than multiple scanner sites, so that participants may be tested in their native environment (Gutchess et al., in press; Ketay et al., 2005; Kobayashi & Temple, 2004). Although this strategy has the benefit of eliminating the possibility of introducing noise due to testing environment alone, it may lack some ecological validity because recent immigrants or bilinguals, through acculturation, may identify more with their current culture during testing and adopt strategies optimal for that cultural environment, thereby reducing the probability of finding cultural variation at the neural level. An alternative strategy is to test participants across multiple scanner sites located in each cultural group's native environment (Chiao et al., 2004). This strategy optimizes ecological validity, because the researchers are also likely to belong to the same culture, enhancing the probability that participants' frame of mind while performing the task strictly relates to their own culture. It is possible that this strategy also introduces another potential confound of variance, namely, differences in signal attributable solely to differences in scanner sites. However, previous neuroimaging studies to examine reliability of fMRI and PET results acquired in different testing sites have found that minimal differences in the data were attributable solely to scanner environment, suggesting that comparing imaging results collected from two different scanner sites

is appropriate and potentially a more advantageous strategy for conducting cultural neuroscience research (Casey et al., 1998; Ojemann et al., 1998).

Culturally Appropriate Brain Templates

Another pressing methodological issue involves the creation of culturally appropriate brain templates for spatial normalization of imaging data and brain atlases used for structure-function mapping. For neuroimaging studies, it is necessary to normalize the images of individual brains to a standard spatial template. Some scientists have argued that brain size and shape significantly vary across different racial groups (Park & Gutchess, 2002). Because the spatial normalization templates and brain atlas used currently (e.g., Montreal Neurological Institute [MNI] space and Talairach Daemon) were created by averaging brain images of predominantly white individuals, it is plausible that these templates are inadequate for capturing subtle but significant variation in brain structure that may subsequently affect where differences in brain function are mapped and observed (Evans et al., 1992; Mazziotta, Toga, Evans, Fox, & Lancaster, 1995; Talairach & Tournoux, 1988). Such considerations may be especially important when studying phenomena that reveal themselves in small areas of brain tissue, such as subnuclei within the amygdala.

Selection of Experimental Measures

A third methodological issue concerns the experimental materials used (e.g., stimuli, task, and procedure). As reviewed earlier in this chapter, cultural psychologists faced many problems in developing sound cross-cultural behavioral measures. In adapting these behavioral paradigms to neuroscience research, several considerations emerge (Aguirre & D'Esposito, 1999). First of all, neuroimaging and electrophysiological experiments typically require many trials depending on the type of design. Because some scientists may want to examine cultural variation in neural responses for tasks in which a behavioral difference has already been demonstrated, an event-related design would be most appropriate so that behavioral responses for each trial can be recorded and mapped onto individual physiological events. In particular, event-related fMRI

designs, which involve recording of behavioral and neural responses on a trial-by-trial basis, typically require more power than block or parametric designs; thus it will be important to include a sufficient number of trials per relevant condition (Buckner & Braver, 1999). Furthermore, tasks, instructions and stimulus displays need to be modified, so that they have equivalent meaning across cultures. When designing neuroimaging studies based on prior cross-cultural behavioral work, special consideration may be given to selecting paradigms that yield a large effect because of the typical smaller sample size in neuroimaging studies relative to cultural psychology behavioral studies. Finally, whereas some of the most effective cultural psychology behavioral paradigms involve tasks that require participants to provide responses beyond a button press (e.g., drawing a line or describing an event), behavioral responses in a majority of current neuroimaging environments are restricted to button presses or vocal responses to minimize potential face and body movement, which can create a significant artifact in the neuroimaging data. Although cultural psychology and neuroscience methods bring unique issues to the experimental design table, each of these issues is resolvable, as suggested by recent progress in cultural neuroscience research.

Genotyping Participants

A fourth methodological concern involves integrating cross-cultural genomic data with neuroimaging. Finding an adequate number of participants (e.g., 15–20) who carry the short- and long-allele version of a given functional polymorphism may require genotyping three times the number of desired participants—particularly for polymorphisms that include a rare version. Once preliminary genotyping has identified an adequate number of participants in both cultures, other neural and behavioral testing can be administered. Integrating genotyping with neural and behavioral assays may have profound explanatory power in explaining cultural differences in neural responses and behavior. For example, significant variation may exist in behavior and/or neural activity between cultural groups; however, further inspection may show that these cultural differences are really driven by differences in ratio of short- to long-allele carriers between cultural groups. Although the pragmatic difficulties of

conducting such research are likely to be great, the potential for discovering new ways of explaining cultural variation across all levels of analysis is tremendous.

IMPLICATIONS OF CULTURAL NEUROSCIENCE FOR BASIC AND APPLIED RESEARCH

The ability for a cultural neuroscience framework to provide novel links between sociocultural and biological phenomenon is unprecedented. The development of paradigms and tools with the three fields of cultural psychology, social-cognitive-affective neuroscience, and imaging genomics make this endeavor possible in ways never previously imagined. We do not expect 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 levels. It is these phenomena that hold the promise to provide a window into our understanding of the interplay of sociocultural and biological forces.

There are at least two foreseeable benefits of a cultural neuroscience approach for basic and applied research: the merging of natural and social sciences, and the enhancement in the condition; and care of human health across different cultural groups.

Merging the Scientific Study of Culture and Biology

The study of culture and biology has long been stratified within universities and academic subfields, creating a deep conceptual and methodological schism between these different communities of researchers. Snow (1959) once hypothesized that molecular biology could serve as a bridge between the two areas of thought. However, only modest progress has been made so far, because genetic-behavior association studies have only been mildly successful. We hypothesize that cultural neuroscience stands in an even greater position to bridge the culture-biology gap by pulling perspectives and methodologies from every area of psychology (from evolutionary and cognitive to cultural and developmental psychology), as well as from the fields of anthropology, molecular biology, and neuroscience. The tools needed to

investigate the links between multiple levels of analysis are available in ways not previously imaginable, and the results of utilizing these tools to investigate phenomena using a cultural neuroscience approach are likely to enable us to articulate with greater specification our conceptions of culture and its mutually influential relationship with biology. The cultural neuroscience framework aims to reshape the trend to specialize and stay within the confines of one's academic subfield toward a transdisciplinary integration of theoretical knowledge and methodological expertise across the social and natural sciences.

Implications for Population Health

The important interplay of culture and genes in the study of population health has long been appreciated (Shields et al., 2005). This belief stems from the fact that significant differences exist in the frequency with which certain health conditions occur across cultural groups. For example, because of "founder effects," Ashkenazi Jewish people have a greater prevalence of Tay-Sachs disease, and cystic fibrosis is more common among people from Northern Europe (Exner, Dries, Domanski, & Cohen, 2001; Wang & Sue, 2005). Another example is population differences in allelic frequency of the gene *CYP2A6*, which affects the likelihood of nicotine addiction (Shields et al., 2005). Protective forms of the *CYP2A6* are very rare in people who self-identify as European or African (less than 3%), but they are more prevalent in people who self-identify as Japanese or Korean (as great as 24%; Shields et al., 2005). How do differences in genetic frequencies affect brain systems and behavior underlying physical and mental health conditions? How do cultural forces affect the expression and function of these genes, and their effect on brain and behavior?

The answers to these intriguing questions are finally within our empirical grasp. Our hope is that the cultural neuroscience framework may be used effectively to identify and investigate candidate phenomena using the prescribed, multiple levels of analytic approach. By integrating across disciplines and methodologies from cultural to biological levels of analysis, we will meaningfully enhance our chances of understanding of how sociocultural and biological forces interact and shape each other, and finding potential ways to direct this knowledge toward timely issues in population health.

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NOTES

1. alfred.med.yale.edu/alfred/aboutalfred.asp
2. This cultural difference at the level of genes is not in the actual makeup of the 5-HTT functional polymorphism, or in how the gene expresses itself, but in the frequency of carriers of the gene or the ratio of people carrying the short- or long-allele version of the gene in the entire population.

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