A Cultural Neuroscience Approach to the Biosocial Nature of the Human Brain

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Cultural neuroscience (CN) is an interdisciplinary field that investigates the relationship between culture (e.g., value and belief systems and practices shared by groups) and human brain functions. In this review we describe the origin, aims, and methods of CN as well as its conceptual framework and major findings. We also clarify several misunderstandings of CN research. Finally, we discuss the implications of CN findings for understanding human brain function in sociocultural contexts and novel questions that future CN research should address. By doing so, we hope to provide a clear picture of the CN approach to the human brain and culture and to elucidate the intrinsically biosocial nature of

During the past few years, brain imaging studies have uncovered variations in the neural substrates of human cognition in different cultural groups. The integration of theory and methods from social and cultural psychology,

CULTURAL NEUROSCIENCE

CN emerges from the integration of different branches of social sciences and natural sciences and arises mainly from two disciplines, i.e., cultural psychology, which has provided the insight that cognitive, emotional, and motivational tendencies and habits are shaped by culture, and neuroscience, which has demonstrated that the brain is shaped by experience. We here show that CN is based on four key approaches, i.e., cultural psychology, social cognitive neuroscience, the study of neuroplasticity, and the study of culture × gene interactions.

Cultural Psychology

Although there is a long history of the debate about the concept of culture (Kroeber & Kluckhohn 1952), it is commonly acknowledged that cultural groups have differentiated over thousands of years to create what has been called cultural speciation (Goodall & Berman 1999). The resulting cultural differences still exist in our globalized world and are associated with certain differences in the ways people think and behave. These differences exist side by side with many cross-cultural commonalities. Cultural differences in human behaviors are very well documented in anthropology (e.g., Haviland et al. 2008), and human development has been viewed as a process of acquiring and embodying culture's belief systems (Rogoff 2003). Cultural differences in human mental processes and underlying cognitive mechanisms have been investigated extensively in cultural psychology during the past two decades. From this line of research, theoretical frameworks such as individualistic versus collectivistic values, independent self-construals versus interdependent self-construals, and holistic versus analytic cognitive tendencies have emerged to guide empirical studies of cultural discrepancy in human cognition and emotion (Kitayama & Cohen 2007, Nisbett et al. 2001, Varnum et al. 2010). Cultural psychology takes the view that human cognitive and affective processes vary as a function of cultural environments that provide unique social contexts in which psychological processes develop and are shaped (Kitayama & Uskul 2011). The findings of cultural psychological research stimulate researchers to investigate neural substrates of cultural diversity of human cognition and emotion.

Independent self-construal: a tendency to view the self as autonomous and bounded; an emphasis on affirming the independence and uniqueness of the self

Interdependent self-construal: a tendency to view the self as interconnected and overlapping with close others; an emphasis on affirming close relationships and maintaining harmony within them

Social Cognitive Neuroscience

Social cognitive neuroscience research investigates brain mechanisms that allow human beings to understand the self and others and to efficiently navigate social environments (Ochsner & Lieberman 2001). Early social cognitive neuroscience research focused on the neural substrates underpinning social cognition by combining brain imaging and social psychological paradigms. Most of these studies aimed to uncover the neural mechanisms of social cognition and behavior without considering potential cultural differences. However, an important feature of social cognition and behavior is context dependence. We are always situationally embedded in a certain environment, the "context," which substantially influences our perception of others and our understanding of the behavior of others. This context dependency itself underlies substantial influences exerted by culture. In other words, what social information is processed and how it is processed rely heavily on one's interaction partners (in the case of dyadic interactions) and, more broadly, on the social context in which the interactions occur. For example, cultural psychological studies have documented numerous variations in social cognitive processes across different cultural contexts, such as construal of the self (Markus & Kitayama 1991, 2010), causal attribution of physical and social events (Choi et al. 1999), analytic versus holistic attention (Masuda & Nisbett 2001), affective states that people ideally like to feel (Tsai et al. 2006), and choice-induced dissonance (Kitayama et al. 2004), among many others. Due to the considerable evidence for cultural divergence of human subjective experiences and psychological processes, recently neuroscientists have shown increasing interest in whether parallel differences in neural mechanisms might also be present

among people who were raised in different sociocultural contexts (Ambady & Bharucha 2009; Ames & Fiske 2010; Chiao & Bebko 2011; Han & Northoff 2008, 2009; Kitayama & Uskul 2011; Park & Gutchess 2006; Park & Huang 2010; Rule et al. 2012). On the theoretical basis alone, cultural influences on the neural substrates underlying human cognitive and affective processes would seem highly plausible given that it takes almost 20 years for a large portion of the brain to mature (Gogtay et al. 2004). During this period the brain is influenced by personal experiences in a specific cultural context. Thus in the beginning of the twenty-first century, researchers started to examine potential cultural differences in human brain mechanisms involved in multiple cognitive and affective processes by comparing brain imaging results obtained from different cultural groups. There is now substantial evidence that individuals from different sociocultural contexts show distinct patterns of brain activity involved in cognition and behavior.

. Biological research has shown ample evidence for the intrinsic plasticity of the human brain; that is, the brain changes both structurally and functionally in response to the environment and experience (Shaw & McEachern 2001). For example, the occipital cortex, which is commonly involved in visual processing in sighted humans, can be engaged in auditory processing in blind individuals (Burton et al. 2002, Gougoux et al. 2009). Auditory deprivation results in the recruitment of the primary auditory cortex in the processing of vibrotactile stimuli (Levanen et al. 1998) and sign language (Nishimura et al. 1999) in deaf humans. The medial prefrontal cortex is engaged during self-reflection on visually but not aurally presented trait words in sighted humans, while the region is recruited during self-reflection on aurally presented trait words in congenitally blind individuals (Ma & Han 2011). These findings demonstrate an intrinsic property of the brain, plasticity, which enables the nervous system to respond to environmental pressures, physiological changes, and personal experiences (Pascual-Leone et al. 2005) and to adapt to social contexts during development (Blakemore 2008). Given that human thoughts and behaviors differ substantially across a variety of sociocultural contexts, it is not surprising that the human brain, the source of human behaviors and the carrier of human thoughts, is modulated by sociocultural environments and develops unique neural mechanisms that help an individual to adapt to culturally specific changes and pressures. Thus an intrinsic feature of the brain is its sociocultural context dependence.

C × . The basic assumption of CN is that culture provides a framework for social behavior, communication, and interaction that generates social values and norms, assigns meaning to social events, interacts with biological variables (e.g., genes), and codetermines the functional organization of the brain. The CN approach investigates mutual interactions between culture, the brain, and genome, consistent with culture-gene coevolution theory (Boyd & Richerson 1985, Lumsden & Wilson 1981). This theory guides research that explores how two complementary and interacting evolutionary processes, i.e., genetic evolution and cultural evolution, influence human behavior. The CN approach aims to understand how sociocultural contexts influence human behavior by examining cultural influences on underlying neural mechanisms. CN views cultural differences in the neural mechanisms underlying cognition as the product of the interaction between genes and cultural environment, an idea that researchers in this field are beginning to test empirically.

Next we review some key concepts related to CN. We provide definitions and also highlight conceptual distinctions between terms such as culture, nationality, and race, which some may mistakenly use interchangeably.

Culture is obviously the most important concept in the field of CN. From

anthropologists' perspective, culture refers to a system of meanings used to make sense of life (i.e., Kuper 1999). Although there are myriad definitions of culture [indeed, Kroeber & Kluckhohn (1952) listed 164 definitions of culture], culture is often used in three basic senses in social psychology (Chiu & Hong 2006). Material culture consists of all material artifacts produced by human beings. Social culture consists of social rules and social institutions. Subjective culture refers to shared ideas, values, beliefs, and behavioral scripts. These aspects of culture, however, are dynamically related within a given cultural tradition, locale, and/or community and together form a unique social environment for the group of individuals. From the very beginning of their life, people engage in the complex composed of materials and social rules or practices as well as folk beliefs of their respective local communities, and by doing so, they have their brains changed in such a way that the resulting brain functions are attuned closely to the surrounding sociocultural environment.

Culture is different from nationality, which is defined by social group membership based on a shared nation state of origin. Although the term culture emphasizes shared ideas, values, beliefs, and practices, people of the same nationality do not necessarily share the same beliefs, values, or practices. Similar to social psychology studies, most CN studies use the term culture in the sense of a social group whose members share social values, knowledge, and practices. Some CN studies have recruited participants from two different cultural groups (e.g., Westerners and East Asians) based on cultural psychology findings that suggest that the two groups differ in specific cultural values or specific cognitive processes. In some cases race and language are concomitants that also differentiate two cultural groups. Other CN studies have investigated two cultural groups who are from the same nation but are defined by religious or political beliefs. In such cases two groups of participants share the same nationality, race, and language but differ only in a set of shared beliefs/values and practices that are hypothesized to be relevant to a particular pattern of neural activity.

Recent CN studies have directly measured cultural values from different groups and have assessed the relationship between these values and neural responses. For example, the Self-Construal Scale (Singelis 1994) has been used in several recent CN studies to evaluate individuals' independent versus interdependent self-construals (e.g., Chiao et al. 2009a, de Greck et al. 2012, Na & Kitayama 2011, Sul et al. 2012). This approach seeks to simultaneously capture both within- and between-group variations instead of assuming, a priori, that people from two sociocultural contexts must have different cultural values. It therefore acknowledges individual differences in cultural values among those who grow up in the same sociocultural context. Moreover, measuring cultural values allows researchers to examine whether a group difference in brain activity is associated with a specific cultural value, whether cultural group differences in brain activity are mediated by a specific cultural value, and how individual differences in brain activity are associated with variations in cultural values within a given cultural group.

Cultural psychology views culture as a dynamic knowledge system rather than a rigid set of stereotypes about a social group (Markus & Hamedani 2007). Culture represents a dynamic concept of the social environment that is not part of the innate biological condition of humans. Humans are not born with propensities for any particular culture but rather with the potential and the capacity to acquire and to create culture (Harris 1999). Thus an individual may change his/her cultural values and beliefs as a result of experience (such as emigrating from his/her native country). People from the same cultural groups can be quite heterogeneous in terms of the values and beliefs they acquire. This is particularly true in contemporary societies where cultural exchanges occur often and rapidly. People in modern societies are rarely monocultural because they are almost always exposed, often deeply, to other cultures' practices and beliefs in multiple sociocultural

contexts. Thus multiple cultural systems may become part of any single individual, and as a consequence, it is often required to switch to and fro between different cultural systems during social interactions depending on specific contexts of social encounters (Hong et al. 2000). This dynamic model of culture allows us to test whether brain activity underlying human cognition can vary on a short temporal scale as a function of recent use of one cultural system or another (e.g., cultural priming, as is discussed in more detail when we turn to the methodology of CN research). Taken together, CN studies view culture as a complex and dynamic external social environment in which the human brain is fostered and shaped. Rather than considering the brain and its neuronal states by themselves, CN emphasizes the sociocultural nature of the human brain and places great weight on the influence of cultural values, beliefs, and practices shared by a social group on functional organization of the human brain.

Race is a way of categorizing human beings on the basis of external attributes, such as skin tone and facial and body shapes, that differentiate human populations. In many racial theories, and in lay theories, racial groups also possess different fixed and biologically determined psychological traits and tendencies. Race is viewed as fixed both over the course of the lifespan and across cultural contexts. People from the same racial group are thought to be homogenous in terms of heritage and physical appearance. However, in reality individuals classified as belonging to the same race do not necessarily share the same cultural values and experiences. For example, Native Chinese and Chinese Americans may be thought to belong to the same racial group but may have distinct cultural values and beliefs and experiences. There has long been a debate over whether racial differences in psychological tendencies and behavior exist and if so whether such differences are biologically determined. As a starting point, there is the question of whether contemporary racial categories can be genetically differentiated. Although some have noted a great deal of genetic similarities across races (humans are 99.9% alike) and argued that it is very difficult to ascertain the racial identity of individuals through their genes (Littlefield et al. 1982), recent large-scale studies using genetic cluster analysis have found correlations between self-reported racial group membership and the genetic cluster of racial groups (e.g., Paschou et al. 2010, Tang et al. 2005). However, these data do not speak to the question of whether racial groups are psychologically different, nor do they address whether such differences (if they exist) are solely or partially genetically driven.

Regardless of whether race has a biological component, race does have a number of complex sociopolitical implications and may be analyzed as a sociocultural construction. Moya & Markus (2011, p. 21) recently defined race as "a dynamic set of historically derived and institutionalized ideas and practices that (1) sorts people into ethnic groups according to perceived physical and behavioral human characteristics; (2) associates differential value, power, and privilege with these characteristics and establishes a social status ranking among the different groups; and (3) emerges when groups are perceived (a) to pose a threat (political, economic, or cultural) to each other's world view or way of life; and/or (b) to justify the denigration and exploitation (past, current, or future) of, and prejudice toward, other groups." In addition, race has a strong evaluative component that has been often used to qualify individuals from different races as superior or inferior on the basis of untested or discredited assumptions related to genetics.

The goal of CN studies is to investigate human brain function and structure in diverse sociocultural contexts. Like cultural psychologists (Markus & Hamedani 2007), CN researchers have little interest in using brain activity as a way to classify people into groups. Instead, CN research investigates whether and how the functional organization of the human brain is shaped by culture and by the interaction between culture and genes on different

time scales (Chiao & Ambady 2007, Han & Northoff 2008). In addition, CN research aims to investigate how neurobiological processes in the human brain contribute to the rise of divergent cultures in the world. Theories built on CN findings will eventually help to explain how cultural differences in human brain function mediate divergent social behaviors across cultures while at the same time pointing out the neural predispositions of psychosocial commonalities across different cultures. CN considers culture as a highly dynamic system of continuous interaction and exchange among individuals. This system of social interaction feeds back into social practices, values, and belief systems, thereby establishing circular, recursive, and reciprocal influences between interacting individuals and culture (Hacking 1999, Vogeley & Roepstorff 2009).

Most current CN studies focus on cross-cultural differences in the neural substrates of human psychological processes including cognition, emotion, and motivation (Ambady & Bharucha 2009; Han & Northoff 2008, 2009; Kitayama & Uskul 2011). This line of research has mainly been stimulated by findings in cultural psychology that show cross-cultural variation in multiple levels of psychological processes (Kitayama & Cohen 2007, Nisbett et al. 2001). By comparing behavioral performances among individuals from Western (e.g., European and American) and East Asian (e.g., Chinese, Japanese, Korean) contexts, cultural psychologists have shown evidence for distinct, culture-dependent cognitive processing styles in perception (Ji et al. 2000), attention (Kitayama et al. 2003, Masuda & Nisbett 2001), memory (Wang & Conway 2004), perspective taking (Wu & Keysar 2007), causal attribution of events (Morris & Peng 1994, Peng & Knowles 2003), object categorization (Ji et al. 2004), recognition of one's own face (Liew et al. 2011b; Ma & Han 2009, 2010; Sui

( ) a noninvasive method for recording blood-oxygenation-level-dependent signals that have high spatial resolution and are used to examine brain activations associated with specific stimuli or tasks

( ) synchronous activities of neuronal populations engaged in specific psychological processing, which are time locked to stimulus events, can be recorded from electrodes over the scalp, and have high temporal resolution

the functional organization of the brain is still lacking. Another line of research has focused on how the allelic frequencies of a genotype within a population may relate to cultural differences in values. Chiao & Blizinsky (2010) examined the relationship between the cultural phenotypes of individualism-collectivism and allelic frequency of the serotonin transporter functional polymorphism (5-HTTLPR) by assessing the prevalence of the short allele of 5-HTTLPR among different populations. In a comparison of 29 countries, they found that cultures that were high in collectivism contained a significantly greater proportion of short allele carriers and that increased frequency of short allele carriers predicted decreased anxiety and mood disorder prevalence. Further, the relationships between the prevalence of short allele carriers within a population and the prevalence of anxiety and mood disorders were mediated by collectivism. Similarly, Way & Lieberman (2010) suggested that collectivism may have developed and persisted in populations with a high proportion of a functional polymorphism (A118G) in the μ-opioid receptor gene—a putative social sensitivity genotype that is compatible with collectivistic cultural groups. Caution is due because this body of evidence is entirely correlational. Nevertheless, given that cultures may interact with the 5-HTTLPR genotypes to influence the prevalence of affective disorders such as anxiety and depression (Chiao & Blizinsky 2010), it would be interesting to study how the culture-gene interaction codetermines the intermediate endophenotype (i.e., neurobiological responsiveness) associated with culture-sensitive cognitive processes.

Although CN is a young field, CN researchers have developed quite sophisticated methodologies by drawing on prior brain imaging and social and cultural psychology research. Methodological challenges include both the design of psychological experiments and brain imaging techniques. Early CN studies focused on whether and how two cultural groups differ in neural substrates of specific cognitive and affective processes. A typical way to address this issue is to compare functional magnetic resonance imaging (fMRI) or event-related potential (ERP) brain data obtained from individuals who were raised in two different sociocultural contexts.

One assumption of this approach is that, because participants from two cultural groups differ in cultural knowledge, values, and/or cognitive and affective processes, the underlying neural activity should be different between the groups in a specific way. To address this assumption, CN research has taken cultural psychological research as a guide for its hypotheses about neural differences between specific cultural groups. For example, behavioral research first showed that individuals in Western cultures are more sensitive to salient foreground objects compared to people in East Asian cultures, whereas individuals in East Asian cultures are more inclined to focus their attention broadly on backgrounds relative to people in Western cultures (Ji et al. 2000, Kitayama et al. 2003, Masuda & Nisbett 2001). Such findings lead to a reasonable hypothesis that neural substrates underlying visual perception of and attention to salient objects and contexts may show different patterns between individuals in the Western and East Asian cultures (Goh et al. 2007, Gutchess et al. 2006, Hedden et al. 2008). Similarly, evidence from cultural psychology that the self is viewed as independent in Western cultures and interdependent in East Asian cultures (Markus & Kitayama 1991, Singelis 1994) leads to the hypothesis that neural representation of the self and close others may overlap to a greater degree among East Asians than among Westerners (Zhu et al. 2007).

However, selection of participants from two different nations or sociocultural contexts does not necessarily imply that the participants have distinct cultural values (Oyserman et al. 2002). CN seeks to address this question by measuring the value or self-construal dimensions that are hypothesized to drive the relevant cultural

differences in the neural process being studied. Often, CN researchers directly assess the cultural values or self-construals of interest; this can be done using well-established questionnaires developed by social and cultural psychologists. For example, the Self-Construal Scale (Singelis 1994) is widely used to evaluate how people view themselves (either as independent or interdependent) and has been shown to differentiate cultural groups. Current CN studies usually compare participants from two countries, usually a Western culture and an East Asian culture (e.g., British versus Chinese, American versus Japanese). Although previous studies have demonstrated differences between these cultures in terms of values and cognitive and affective processes, it is important to demonstrate that the participants recruited in CN studies actually differ in these dimensions. Measurements of cultural values are also helpful in situating CN studies as dealing with cultural differences rather than racial or national differences. Equally important, measuring cultural values allows for stronger inferences. By examining whether individual differences in cultural values can predict individual differences in brain activity, researchers can probe the association between these values and patterns of brain activity. In addition, measuring cultural values in individual subjects makes it possible to assess whether cultural values mediate differences in brain activity associated with specific tasks, which may be performed in different ways according to the respective degree of the cultural value, between two cultural groups.

Of course, when comparing participants from different sociocultural contexts, it is important to control for potentially confounding variables such as gender, age, and education as well as socioeconomic status. Language is another potential confound in cultural comparisons if stimuli used in brain imaging studies are based on verbal materials. This, however, can be controlled by using the native language for each cultural group so that the same language is used in an experimental condition and a control condition. Such designs allow us to compare the experimental and control conditions so as to reduce the effect of language processing to a minimum degree.

Another elegant psychological paradigm used by CN researchers is to prime cultural identity or values before recording brain activity during a specific task. Such studies are based on the assumption that individuals can acquire more than one set of cultural knowledge and can use different sets of cultural knowledge depending on contextual cues (Hong et al. 2000). According to this dynamic constructivist model of culture, people who have been exposed to multiple cultures may acquire multiple sets of cultural knowledge, and exposing individuals to cultural symbols may activate specific cultural knowledge and result in mindsets and behaviors that are consistent with that culture. For instance, after cultural priming, bicultural individuals may switch between Western and East Asian mindsets that are consistent with the most accessible cultural knowledge tradition (e.g., Hong et al. 2003). A number of studies have also shown that priming independence and interdependence of self-construals influences patterns of cognitive processes that tend to differ between cultural groups (e.g., Kühnen & Oyserman 2002, Lin & Han 2009;

than site effects when participants are scanned using the same type of scanner at two sites (Sutton et al. 2008). For those CN studies that scan multiple cultural groups at different sites, Chiao et al. (2010) has suggested several ways to reduce the probability of systematic, site-dependent effects in fMRI sensitivity. First, both functional and anatomical MRI data should be collected using scanners from the same vendor with identical protocols. Second, an interscanner reliability test can be conducted by scanning a separate cohort of participants or phantom data at each scanner facility, thus enabling one to quantify and statistically compare signal-to-noise ratio across scanner sites. Third, the presentation software and hardware should be identical, calibrated and tested at each session, and scripts should be written and implemented across the sites in a culturally appropriate manner.

Relative to fMRI, electroencephalogram (EEG) is a simpler method for cross-cultural comparisons of brain activity. Similar EEG recording systems can be found easily at different recording sites. Portable EEG amplifiers are available and can be easily transferred between different recording sites so that EEG data from different cultural groups can be recorded using the same system. Analyzing ERPs that are time locked to a stimulus or a response is particularly helpful for uncovering the time course of neural responses to multiple cognitive processes such as recognition of one's own face (Sui et al. 2009, 2012), inference of one's own and others' personality traits (Mu & Han 2010, Na & Kitayama 2011), implicit processing of vocal tone (Ishii et al. 2010), emotion regulation (Murata et al. 2012), and musical processing (Nan et al. 2006, 2009).

Several recent review articles have summarized major findings from CN research (e.g., Ambady & Bharucha 2009; Ames & Fiske 2010; Chiao & Bebko 2011; Han & Northoff 2008, 2009; Kitayama & Uskul 2011; Park & Huang 2010; Rule et al. 2012). Thus this section is not intended to give an extensive review of current CN findings. Instead, we highlight a select set of recent CN studies in terms of their methodology in order to illustrate the intellectual development of CN research.

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. One question that CN researchers are interested in is how human brain activity is tuned by culturally familiar/unfamiliar information. To address this, CN researchers simply recorded neural activity to culturally familiar/unfamiliar stimuli from one cultural group. For example, to investigate the neural basis of musical phrase boundary processing during the perception of music from native and nonnative cultures, Nan et al. (2008) used fMRI to record brain activity in German musicians while they categorized phrased Western and Chinese musical excerpts. They found that culturally familiar musical excerpts more strongly activated multiple brain regions including the superior frontal gyrus, the posterior precentral gyrus, and the superior temporal gyrus, possibly reflecting enhanced sensorimotor integration. Culturally unfamiliar musical excerpts, however, more strongly activated the posterior insula as well as the middle frontal and angular gyri, possibly due to higher demands on attention systems and higher loads on basic auditory processing. Similarly, Demorest & Osterhout (2012) recorded ERPs while American participants listened to melodies based in the Western folk tradition or North Indian classical music. ERPs showed that a long latency positive activity was sensitive to the original and deviation form of the melodies, and this effect was more salient in the Western than in the Indian context. The results suggest that people may generate specific expectancies when listening to culturally familiar music, whereas they may remain unable to develop such expectancies when hearing culturally unfamiliar music.

Another example of this line of research examined whether observations of culturally familiar/unfamiliar symbolic gestures engage distinct neural subsystems. Liew and colleagues (2011a) scanned Chinese participants while

they perceived video clips in which a model showed culturally familiar/unfamiliar symbolic gestures. They found that culturally familiar gestures increased activity in the posterior cingulate cortex, the dorsal portion of the medial prefrontal cortex and the bilateral temporoparietal junction. These brain regions constitute the neural circuit engaged in inference of others' intentions and beliefs (Frith & Frith 2006). In contrast, unfamiliar gestures generated activity in the left inferior parietal lobule, the left superior frontal gyrus, and the bilateral superior parietal lobule. These brain regions make up the neural network involved in automatic motor simulations of observed actions (Rizzolatti & Sinigaglia 2010). Apparently, the mentalizing system is engaged during observation of culturally familiar gestures in order to understand others' intentions or beliefs, whereas the mirror neuron system may be activated during perception of culturally unfamiliar gestures so as to capture others' mind through automatic motor simulations of observed actions. Taken together, these findings indicate that long-term cultural experiences may result in specific neural mechanisms in the human brain that deal with culturally familiar information. This may allow the individual to quickly comprehend the meaning of social information in one's own culture, predict others' behavior, and take appropriate actions in a specific cultural context.

. The mainstream of CN studies focuses on whether differences in cognitive processes between two cultural groups revealed by cultural psychology are associated with distinct patterns of brain activity. There is now increasing evidence that two cultural groups may employ distinct neural mechanisms while performing seemingly identical cognitive and emotional tasks. This is of fundamental importance to understanding brain-behavior relationships in general as well as to CN. There are two patterns of cultural group difference in the neural activity involved in cognitive and affective processes.

One type of cultural modulation of brain activity is that a specific neural activity is significantly modulated by a particular task in one cultural group but not in another cultural group. Based on the assumption that Westerners tend to attend to salient objects whereas East Asians are inclined to attend to a broad perceptual and conceptual field (Nisbett et al. 2001, Nisbett & Masuda 2003), Jenkins et al. (2010) tested whether the neural activity in the lateral occipital cortex to a target stimulus was more sensitive to background scenes in East Asians than in Westerners. They scanned American and Chinese participants during perception of pictures consisting of a focal object superimposed upon a background scene that was congruent (e.g., a deer in the woods) or incongruent (e.g., a television in the desert) with the target object. The target object was presented on different novel scenes or on a single repeated scene on four successive trials. Adaptation magnitude was calculated by subtracting the neural activity to objects on a repeated scene from that to objects on different novel scenes. Jenkins et al. found that the neural activity in both the right and left lateral occipital cortex showed significantly greater adaptation to incongruent scenes than to congruent scenes, suggesting sensitivity of the occipital activity to the background scenes. However, this effect was evident in Chinese participants but not in American participants. Similar results were observed in another study that recorded ERPs to target objects that were presented on semantic congruent or incongruent background scenes (Goto et al. 2010). It was found that a negative ERP component peaking at about 400 ms after stimulus onset (N400), which has been shown to be sensitive to processing semantic relationships (Kutas & Hillyard 1984), was enlarged by target objects presented on semantically incongruent versus congruent background scenes; however, this effect was observed in Asian Americans but not in European Americans.

This pattern of cultural differences was also observed in neural activity involved in high-level social cognition. To investigate cultural differences in the neural mechanisms

. the cortical junction zone at the border of the posterior parts of the temporal lobe and the inferior parts of the parietal lobe, which has been shown to be involved in belief reasoning and perspective taking

00 . a negative potential that peaks around 400 ms after stimulus onset with the maximum amplitude over the parietal scale site and is sensitive to semantic incongruity between stimuli

underlying causal attribution of physical events, Han and colleagues (2011) first scanned Chinese participants during causality versus

( ) the medial region of the prefrontal cortex that has been shown to be involved in social cognition, with the dorsal region engaged in mental state reasoning and the ventral region engaged in self-reflection

mechanisms that are observed in one culture but not in others.

Another type of cultural modulation of brain activity is that a specific neural activity is modulated by a particular task in two cultural groups but in opposite ways. These opposite patterns of neural activity may have nothing to do with the cultural familiarity of the stimuli, but may instead reflect culturally specific cognitive styles. Hedden et al. (2008) assessed cultural differences in the neural activity underlying attentional control by scanning East Asians and Americans in context-dependent or context-independent judgment tasks. Participants were presented with a series of stimuli, each consisting of a vertical line inside a box. The context-dependent task required judgments of whether the box and line combination of each stimulus matched the proportional scaling of the preceding combination. The context-independent judgment task required judgments of whether the current line matched the previous line, regardless of the size of the accompanying box. It was found that the neural activity in the prefrontal and parietal cortices involved in the tasks showed an opposite pattern of activations in the two cultural groups; that is, Americans showed greater prefrontal and parietal activity during the context-dependent than context-independent tasks, whereas East Asians exhibited stronger activity in the prefrontal and parietal cortices during the context-independent than context-dependent tasks. The opposite pattern of neural activity was interpreted as reflecting enhanced sustained attentional control during culturally nonpreferred in comparison with preferred tasks.

Opposite patterns of neural activity in two cultural groups may also arise from distinct cultural values. To examine why American culture tends to reinforce dominant behavior whereas Japanese culture tends to reinforce subordinate behavior, Freeman et al. (2009) scanned American and Japanese individuals during perception of body displays related to dominance and subordination. The neural activity in the bilateral caudate nucleus and MPFC showed an opposite pattern of modulation by the stimuli in the two cultural groups. Americans showed greater activity in these brain regions when perceiving dominant stimuli than when perceiving subordinate stimuli, whereas the reverse pattern of neural activity in the same brain regions was evident among Japanese. Consistent with the fMRI results, Americans self-reported a tendency toward more dominant behavior, whereas Japanese self-reported a tendency toward more subordinate behavior. Moreover, activity in the right caudate and MPFC correlated with behavioral tendencies toward dominance versus subordination. The findings suggest that functional activity in the mesolimbic reward system is modulated in different (and opposite) ways in order to coordinate with cultural preferences for dominant or subordinate behavior.

Taken together, these brain-imaging findings indicate that the same neural substrates are tuned to a particular task in opposite patterns in different cultures. This may reflect the effects of culturally specific cognitive styles or values. These findings are in concordance with contemporary social psychological models of cultural differences in cognition and provide possible neural accounts of previously observed cultural differences in psychological tendencies and behavior. As discussed below, in many of these studies explicit effort has been made to link the cultural difference to underlying values, self-construals, and/or acculturation levels. Hence, it is neither race nor nationality per se, but rather pertinent psycho-cultural dimensions such as independence/interdependence, individualism/collectivism, or hierarchical/egalitarian orientations that modulate the brain activities that are observed. Thus the concept of race may be regarded as irrelevant on the empirical level. Moreover, none of the aforementioned CN findings can be simply attributed to differences in physical appearance, if any, between different cultural groups.

Other CN studies have investigated cultural influences on neural activity by comparing subcultural groups within a single national culture. For example, Han et al. (2008, 2010) examined whether and how religious beliefs

as cultural practice modulate the neural mechanisms underlying self-reflection. They scanned Christian and nonreligious Chinese participants during personal trait judgments of the self and a celebrity and found that in nonreligious Chinese, self-judgments activated the ventral MPFC, a region that is associated with coding the self-relevance of stimuli (Han & Northoff 2009, Northoff et al. 2006). In contrast, in Christian Chinese, self-judgments activated the dorsal MPFC, a brain region that is engaged in inference of others' mental states (Grèzes et al. 2004). The results suggest that religious beliefs produce significant effects on the functional organization of the MPFC in self-reflection independently of race (and also language and nationality). Similarly, using an ERP paradigm, Varnum et al. (2012) found differences in neural responses indicating spontaneous trait inference when comparing European Americans from working-class and middle-class backgrounds that are parallel to differences between those observed between European Americans and East Asians using the same paradigm (Na & Kitayama 2011).

. Increasingly, CN researchers have noticed that it is not enough to show cultural group differences in brain activity involved in a specific task. It is also important to test whether neural activity varies across individuals with different cultural values and whether an observed cultural group difference in brain activity is mediated by a specific cultural value. This line of research helps to further uncover the mechanisms of cultural modulation of human brain activity.

Even individuals from the same cultural groups may differ in many culture-related values and behaviors. Thus it is a novel issue whether observed brain activity in a specific task is associated with a cultural value across individuals. For example, given the difference in self-construals between Western and East Asian cultures (Markus & Kitayama 1991), recent CN studies have investigated whether the variation of brain activity across individuals is associated with one's self-construal. Self-construal styles can be estimated using the Self-Construal Scale (Singelis 1994), which assesses individual differences in independent/interdependent self-construals. Goto et al. (2010) found that the modulation of the N400 amplitude to target objects by semantically incongruent versus congruent background scenes was stronger in Asian Americans than in European Americans. They also showed evidence that smaller-magnitude N400 incongruity effects were associated with higher independent self-construal scores across the whole subject sample.

Other CN studies found an association between self-construal measurements and brain activity that is directly related to the processing of self-related information. Chiao et al. (2009a) studied Japanese and Caucasian Americans using a general self-referential task (i.e., to judge whether a sentence can describe oneself in general) and a contextual self-referential task (i.e., to judge whether a sentence can describe oneself in a specific context). They found that MPFC activity during contextual versus general self-judgments was positively correlated with self-reported collectivism/individualism. Similarly, Sul et al. (2012) examined the neural substrates underlying self-reflection in Koreans with different cultural orientations and showed that interdependent self-construals predicted stronger activation in the left superior temporal gyrus related to personality trait judgments. These findings provide evidence that individual differences in brain activity can be associated with a specific cultural value.

While some CN studies have shown cultural group differences in both brain activity and a specific cultural value (e.g., de Greck et al. 2012, Goto et al. 2010), other CN studies have tried to address whether cultural values mediate differences in neural activities that differentiate between two cultural groups. This has been tested using mediation analysis (MacKinnon et al. 2007), which can assess whether a mediating variable transmits the effect of an independent variable on a dependent variable.

To examine cultural effects on neural responses to target objects and stimulus context, Lewis et al. (2008) recorded ERPs from European and East Asian Americans while they responded to a target stimulus (the number 6) and ignored frequent nontarget stimuli (three-character words or numbers) and an infrequent nontarget stimulus (the number 8). A cultural value was measured using the Individualism and Collectivism Attitude Scale (Triandis 1995). Independent self-construal was measured by calculating the average response on the Individualism subscale, and interdependent self-construal was measured by calculating the average response on the Collectivism subscale. They first showed that European Americans displayed relatively greater P3 amplitudes to target events, whereas East Asian Americans displayed relatively greater P3 amplitudes to the infrequent nontarget stimulus (novelty P3). They further found that culture predicted self-construal (the East Asian Americans were significantly more interdependent than the European Americans) and the P3 novelty

as cultural primes. Chinese cultural priming decreased MPFC activity that differentiated between trait judgments of the self and mother, whereas Western cultural priming produced the opposite effect. Such dynamic variation of the neural correlates of the self is consistent with previously observed differences in the neural representations of the self between Chinese and Westerners that reflects the chronic influences of cultural values and practices.

Another line of priming research has focused on manipulating cultural values that are hypothesized to underlie group differences in neural function. For example, Sui & Han (2007) used self-construal priming (Gardner et al. 1999) with a group of Chinese participants, asking them to search for independent or interdependent pronouns (e.g., "I" or "we") in essays. They showed that the right frontal activity related to recognition of one's own face was significantly reduced after the interdependent versus independent self-construal priming. This finding indicates that the neural process involved in recognition of one's own face is shaped by dynamic variation of self-construals. Self-construal priming has also been shown to modulate neural activity related to early perceptual processing (Lin et al. 2008). In this study, Chinese participants were primed with independent or interdependent self-construals before discriminating global or local features of hierarchical stimuli. The ERP results showed that independent self-construal priming resulted in larger occipital P1 amplitudes to local targets than to global targets, whereas a reverse pattern was observed after the interdependent self-construal priming. Similarly, Chiao et al. (2009a) primed Asian Americans using the Sumerian Warrior Story Task and the Similarities and Differences with Family and Friends Task (Trafimow et al. 1991), which have been shown to influence self-construal. They found that priming individualistic values increased activation in the ventral MPFC and posterior cingulate cortex during general self-judgments relative to contextual self-judgments. Priming collectivism led to the opposite pattern. Thus the findings from priming studies indicate that cultural values dynamically shape neural representations of the self and close others.

How does temporary access to other cultural frameworks interact with long-term cultural experiences to shape human brain activity? In an initial attempt to answer this question, Sui and colleagues (2012) recorded ERPs from British and Chinese adults during judgments of orientations of one's own and a friend's faces after they were primed with independent and interdependent self-construals. They found that priming an interdependent self-construal reduced the default anterior N2 in response to their own faces for British participants. By contrast, priming an independent self-construal suppressed the default anterior N2 in response to their friend's face for Chinese participants. These findings illustrate how temporary and chronic cultural orientation may interact to shape neural responses. Chronic cultural orientation may constrain the effect of cultural priming on brain activity, reflecting a complex pattern of interactions between short-term and long-term cultural experiences.

In sum, CN findings are obtained using three distinct sets of methods. Initial demonstrations of cultural differences in brain activity focus on comparisons between individuals from two cultural groups (e.g., East Asians and Westerners). This type of work suggests that sociocultural contexts may result in different patterns of brain activity related to human cognition. These initial demonstrations are often followed by further analyses on underlying value or self-construal dimensions, providing further evidence that the observed cultural group differences in brain activity are associated with specific cultural values (e.g., self-construals). A similar extension has also been attempted with priming (manipulating the salience of either culture or important cultural values) to test whether there are causal relationships between culture and the neurocognitive processes involved in human cognition. In addition to showing a causal role of cultural values and self-construals, the priming studies have

. a procedure that allows self-construal to shift either to an interdependent or an independent style in a given population (e.g., by reading essays with the instruction to focus one's attention on personal pronouns either in the singular or plural form)

demonstrated that culturally typical patterns of brain activity are sometimes quite malleable.

The rapid development of CN has induced several misunderstandings of CN research. These misunderstandings relate to the origin of CN research, the biological versus social nature of the human brain, and the relationship between culture and race (e.g., Mateo et al. 2012).

One misunderstanding of CN research is to connect CN studies with anthropological approaches to explain the nature of culture, which produces the misimpression that the goal of CN studies is simply to find biological markers in the brain that differentiate cultural groups and to demonstrate that any cultural differences in brain activity are determined biologically and are immutable. Such misunderstanding also arises from an ontologically dualistic opposition of the biological and cultural nature of the human brain. Such a false dichotomy leads to a view of biology and culture as two opposite accounts of the nature of the human brain. CN actually has a nonreductionist view of the relationships between formative biological and cultural properties of the human brain. As previously noted, CN studies aim to elucidate neuroplastic and culturally generated processes. This is fundamentally at odds with cultural essentialism and hard-wired biological determinism. CN researchers generate specific hypotheses about neurocognitive processes grounded in both behavioral findings from cultural psychology and brain imaging findings from cognitive neuroscience. These hypotheses limit the brain regions under investigation and predict specific patterns of cultural group differences and individual differences in brain activity. Thus CN research does not study culture as a set of biologically determined predispositions/constraints that can be used to rigidly categorize collections of people. Instead, the CN approach emphasizes the flexibility of the human brain that enables humans to adapt to sociocultural environments.

Another misunderstanding of CN arises from the confusion between culture and race. While some CN studies have compared participants from cultural groups that are also purported to be racial groups, other CN studies have examined cultural effects such as differences in brain activity between religious groups and between social classes of the same race. CN assumes that any difference between these groups is primarily the result of socialization and chronic cultural experiences. None of the aforementioned CN findings can be simply explained by group differences in physical attributes (e.g., skin tone). CN studies have shown evidence that differences in brain activity between Westerners and East Asians can be mediated by specific cultural values (e.g., independent versus interdependent self-construals). Cultural priming research has demonstrated causal effects of culture on brain activity. These findings indicate the importance of neuroplasticity in the study of culture and demonstrate that culture is not viewed as an analog for race in CN research.

The confusion between culture and race may lead to allegations of racism against CN research (e.g., CN findings "exert a tremendous impact on the reproduction of stereotypes and racism"; Mateo et al. 2012, p. 158). Racist accounts of human difference hold that human traits are biologically determined, fixed, and that members of racial groups are homogenous in these traits. In stark contrast to these beliefs, CN researchers view a cultural group as a dynamic collection of individuals who share a similar sociocultural context and whose members are affected by that context in divergent ways (a view shared by cultural psychologists; Heine 2012). CN research regards human neurocognitive processes as being flexible and being continuously shaped by sociocultural environments. CN findings demonstrate that an individual's brain is not doomed by biology to work in a specific way, but rather that the brain is strongly shaped by long-term and short-term cultural experiences. It is sociocultural context rather than race that matters. Knowing about cultural differences in neurocognitive processes

may discourage people from believing biologically essentialist accounts of race and thus may facilitate cross-cultural communication. In this sense, CN studies should help to reduce rather than facilitate the reproduction of stereotypes and racism.

CN findings have a host of both theoretical and practical implications. Here we list a few of them. First, CN studies reveal the culturally sensitive nature of the human brain and help us to understand how the human brain as a biological organ is shaped by man-made sociocultural contexts. Human beings are different from other animals in that humans create the most complicated and varied social environments. We are also unique in our capacity for culture. Although there are cultural universals, the specific contents of culture are greatly important. In comparison with other species, this is an important advantage for the development of culture in a generalized sense as social communities of conspecifics. Every person is fostered in a unique artificial environment, speaks his/her mother language, behaves in accordance with specific social rules, acts as a member of social institutions, and interacts with people who share specific cultural values with each other. Thus the human brain develops in a specific sociocultural context during interactions with others. Because there are large variations across cultures, how to fit into one's specific society and how to cooperate with others efficiently is a challenge for each person. CN studies indicate that the human brain has the capacity to develop culture-specific neurocognitive processes that help an individual to function in a specific sociocultural environment.

Second, the context-dependent nature of the human brain can be understood in two different senses. One possibility is that the culturally different stimuli merely modulate already preexisting neural activity that, as such, remains independent of any contextual effects. This amounts to what has been called modulatory context dependence (Han & Northoff 2008, Northoff 2012). Alternatively, the constitution of any neural activity is dependent upon the context; this amounts to what can be described as constitutive context dependence (Han & Northoff 2008, Northoff 2012). The distinction between these two conceptions of context dependence has far reaching implications for the relationship between biological and social domains. In the case of modulatory context dependence, neuronal and social activities interact with each other while remaining independent from each other in their respective constitution. The brain is then purely neuronal and thus biological, whereas culture is social. This differs from the model of constitutive context dependence, which posits that, if the constitution of the brain's neuronal activity depends on the respective social context, a clear-cut distinction between the biological domain of the brain and the social domain of culture is impossible. Rather than being exclusively and completely biological, the brain and its neuronal activity must then be considered to be a hybrid of both biological and social influences. In other words, our brains are biosocial. The brain is then a relational organ that bridges the gap between the biological world of the organism and the social world of the environment and its culture (Northoff 2012).

Third, CN findings help us to understand cultural differences in human behaviors. Traditionally, there was usually a dominant culture in a given society, and contact with out-groups was limited. Cognition and behavior adhere to the cultural environment, and this may result in cultural imprinting effects on the brain. In current societies, however, it is much easier for people to meet members of many different cultures. One issue raised by CN studies is what kind of experiences during development may facilitate the ability of individuals' brains to fit into their specific culture and to interact with individuals from other cultures. This is particularly important for those who emigrate to another culture. Does the brain adapt to a new culture, and if so, how quickly? CN studies, particularly

those using cultural priming, suggest that even an adult's brain is quite flexibly attuned to socio-cultural environments. Thus cultural education and experience may shape the brain in order to fit into new cultural contexts.

operate not only on the functional neural level but also on the biochemical level.

CN research also needs to be integrated with genetic imaging. Although imaging studies have shown both cultural and genetic effects on brain function, there has been little research that examines whether and how culture and genes interact to affect neural processes. One possible approach to this issue is to examine genotype and culture simultaneously using brain imaging. Studies along this line will offer a comprehensive description of how culture and genes interact to shape the human brain and may further challenge purely biological accounts of the brain.

. The increasing number of immigrants in the current society raises another important issue for CN research: Is there a sensitive period during development for acculturation of the brain? Recent behavioral research suggests that, for individuals who immigrated before approximately age 14.5, identification with a new culture increased with time living in the new culture (Cheung et al. 2011). However, for older immigrants, identification with a new culture seemed not to change with the time in the new culture. Such findings imply that there may be a sensitive period for acculturation of the human brain. Among individuals of different ages, this can be examined by investigating the variation of brain activity as a function of the time spent in a new culture.

. CN studies also raise issues concerning cross-cultural differences in the prevalence (and neural correlates) of psychiatric disorders such as schizophrenia and depression. Although these mental disorders appear to occur with similar lifetime prevalence in different cultures, it remains unclear whether their symptomatic expression is influenced by cultural predispositions (e.g., collectivism versus individualism) and whether their symptomatology is mediated by similar patterns of abnormal neural activity. Do the same neurocognitive mechanisms mediate these psychiatric disorders across cultures? Further, is the association between genotype and mental illness similar across cultures, or is it moderated by cultural context? Answering these questions may help to determine whether the same treatments are appropriate for mental disorders in different cultures.

. Finally, one of the main goals of CN research is to address how the brain is involved in the creation and maintenance of the cultures that exist today. This may seem like a research question that is beyond the grasp of CN. However, CN studies may create new paradigms to distribute values and practices in a small group of participants and examine whether and how such manipulations may result in corresponding changes in brain activity. Such an approach may provide the ability to directly test neuroscience accounts of cultural differences. Further, such an approach may provide insights into how culturally influenced ways of thinking and feeling are acquired and represented in the human brain.

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This review presents a refined account of CN in terms of origin, concept, method, findings, and theory, and clarifies several misunderstandings of the field. In sum, CN investigates the biosocial nature of the human brain by examining whether and how implicit and explicit patterns of beliefs, values, meanings, and practices in specific sociocultural contexts shape the neural mechanisms underlying human cognition, emotion, and behavior. CN research has helped to provide a nuanced understanding of culture by integrating methods from social and cultural psychology and neuroscience. The accumulating findings in the field show strong evidence for cultural influences on the human brain and raise exciting new questions about the biosocial nature of human beings. We believe that the continued growth and development of CN will promote cross-cultural understanding and provide strong evidence against racist accounts of human difference.

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