

Cultural Neuroscience of Social Cognition

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Abstract A contemporary mystery for both social neuroscientists and social cognitive neuroscientists has been to distill the core mechanisms in the human brain that facilitate complex social behavior. The purpose of this chapter is to examine this mystery from a cultural neuroscience perspective. Opening with a description of the social brain hypothesis, the chapter first describes research on the neurobiological basis of human social behavior, as well as an account of the culture–gene coevolutionary theory. In the next section, the chapter examines the theory and methods used by cultural neuroscientists to investigate the development of the social brain over the course of culture–gene coevolution. This section reviews recent evidence for cultural influences on social cognitive brain function across a range of domains from self-knowledge and interpersonal perception to empathy and theory of mind. Finally, the chapter ends with questions open to future research endeavors using cultural neuroscience methods to examine social cognition.

Keywords Culture-gene coevolution · Cultural neuroscience · Social cognition

1 The Social Brain Hypothesis

Humans, like non-human primates, live in incredibly complex social groups of varying size from small-scale hunter-gatherer tribes, ranging from a few to a few hundred people, to large-scale settled horticultural tribes, ranging from a few hundred to a few thousand people. According to the social brain hypothesis, such versatility in social living

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arrangements is possible due to increased growth in brain size, particularly in the neocortex (Brothers 2001; Dunbar 1998). That is, humans, like other primates, have evolved an unusually large brain with increased cognitive capacities in order to meet the demands of living in unusually complex social structures. Supporting this view, a number of quantitative studies have shown that, among primates, the relative volume of the neocortex is positively correlated with a range of markers of social group complexity, including the average size of a social group, number of females in the group, grooming group size, frequency of coalitions, prevalence of social play, prevalence of deception, and frequency of social learning (Dunbar and Shultz 2007). These findings provide initial support for the notion that the human brain has evolved for social group living. A contemporary mystery for social neuroscientists and social cognitive neuroscientists alike has been to distill the core mechanisms in human brain that facilitate complex social behavior, by mapping networks of brain structures to complex social functions.

Over the past decade, social neuroscientists have been unraveling the structure and function of the social brain with remarkable success (Adolphs 2009; Decety and Cacioppo 2010; Hein and Singer 2008; Ochsner and Lieberman 2001; Ochsner 2007). Convergent evidence from functional neuroimaging and patient studies indicates that a network of brain regions subserve a range of processes that enable humans to infer the thoughts, feelings and desires of others and themselves, including the medial prefrontal cortex (MPFC), anterior cingulate cortex (ACC), anterior insula (AI), secondary somatosensory cortex (SII), temporal poles (TP), superior temporal sulcus (STS), and temporo-parietal junction (TPJ) (see Fig. 1). Seemingly complex

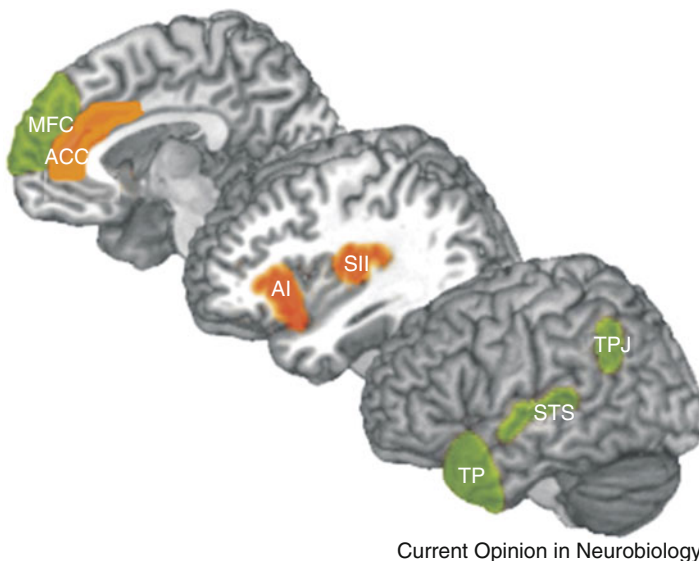


Fig. 1 Illustration of network of brain regions involved in understanding the mental states of self and others (adapted from Hein and Singer 2008). *MFC* medial prefrontal cortex, *ACC* anterior cingulate cortex, *AI* anterior insula, *SII* secondary somatosensory cortex, *TP* temporal poles, *STS* superior temporal sulcus, *TPJ* temporo-parietal junction

social skills such as inferring another's desires or beliefs in the absence of sensory input are supported by neural activity within the right TPJ (Saxe and Kanwisher 2003), while sharing the emotional pain of a close other is facilitated by neural activity within the ACC and bilateral insula (Singer et al. 2004). The ability to think about one's self and distinguish it from another is supported by neuronal activity within cortical midline structures such as the MPFC and posterior cingulate cortex (PCC) (Northoff et al. 2006), while the ability to recognize fear in another's face relies on ensembles of neuronal activity within the human amygdala (Adolphs 2009).

In addition to identifying reliable mappings between brain structure and function, social neuroscientists have also begun uncovering the genetic mechanisms that have evolved to regulate social brain functioning. In particular, the serotonin transporter gene (SLC6A4) has been implicated in emotional and social processing (Canli and Lesch 2007). The serotonin transporter gene (SLC6A4) contains a polymorphic region, known as 5-HTTLPR, comprised of a short (S) allele and a long (L) allele version that result in differential 5-HTT expression and function (Lesch et al. 1996). Individuals carrying the S allele of the 5-HTTLPR produce significantly less 5-HTT mRNA and protein, resulting in higher concentrations of serotonin in the synaptic cleft relative to individuals carrying the L allele (Lesch et al. 1996). Evidence from behavioral genetics indicates that the S allele of the serotonin transporter gene (5-HTTLPR) is associated with increased negative emotion, including heightened anxiety (Munafò et al. 2005; Sen et al. 2004), harm avoidance (Munafò et al. 2005), fear conditioning (Lonsdorf et al. 2009), attentional bias to negative information (Beevers et al. 2007), as well as increased risk for depression in the presence of environmental risk factors (Caspi et al. 2003; Taylor et al. 2006; Uher and McGuffin 2008; see also Munafò et al. 2009). By contrast, people who carry the L allele are thought to have higher degrees of agreeableness (Lesch et al. 1996). Convergent evidence indicates that activity in brain regions that are regulated by serotonergic neurotransmission and are critical to emotional behavior, such as the amygdala, varies as a function of 5-HTT. Specifically, individuals carrying the S allele show greater amygdala response (Hariri et al. 2002; Munafò et al. 2008), which is likely due to increased amygdala resting activation (Canli et al. 2005) and decreased functional coupling between the amygdala and subgenual cingulate gyrus (Pezawas et al. 2005), relative to those carrying the L allele. Comparative primate studies indicate that macaque societies that are more hierarchical and less tolerant are polymorphic for the 5-HTTLPR relative to those who are more egalitarian and conciliatory (Thierry et al. 2000). Hence, the serotonin transporter gene plays a key role in regulating neural mechanisms underlying emotional and social behavior in humans and other primates.

While great progress has been made over the past decade in understanding the neurobiological basis of human social behavior, an important puzzle remains. Prior research in social neuroscience to date has focused largely on the role of natural selection in shaping adaptive mechanisms in the human mind and brain that facilitate social group living and are largely shared across cultures. For instance, a central goal of social neuroscience research to date has been seeking evidence for social brain modules or cortical regions specialized for social cognitive functions (Adolphs 2009). One of the most compelling cases for social

brain modules is the fusiform face area (FFA), a region within extrastriate cortex that responds preferentially to faces relative to other kinds of complex visual stimuli (Kanwisher et al. 1997).

However, more recently, culture–gene coevolutionary theory has emerged as a complementary process by which adaptive mechanisms in the human mind and brain may have evolved to facilitate social group living through both cultural and genetic selection. In particular, culture–gene coevolutionary theory posits that cultural traits are adaptive, evolve, and influence the social and physical environments under which genetic selection operates (Boyd and Richerson 1985). A prominent example of dual inheritance theory across species is the culture–gene coevolution between cattle milk protein genes and human lactase genes (Beja-Pereira et al. 2003) whereby the cultural propensity for milk consumption in humans has led to genetic selection for milk protein genes in cattle and gene encoding lactase in humans.

Recently, Chiao and Blizinsky (2010) uncovered novel evidence for culture–gene coevolution in humans. Specifically, they found that cultural values of individualism and collectivism are associated with the serotonin transporter gene (*5-HTTLPR*) across nations (Fig. 2). Collectivistic cultures were significantly more likely to be comprised of individuals carrying the S allele of the *5-HTTLPR* across 29 nations.

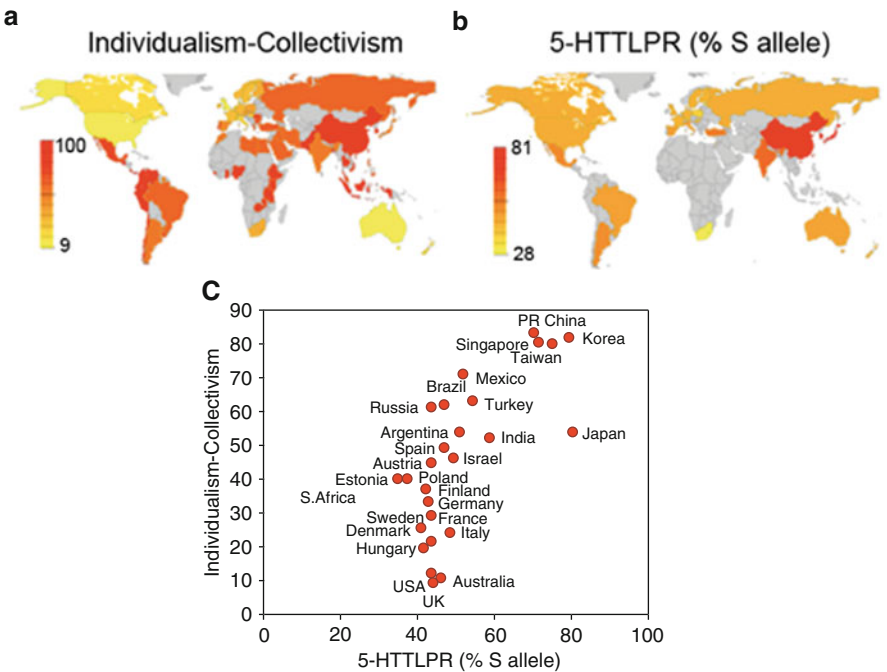


Fig. 2 Culture–gene coevolution of individualism–collectivism and the serotonin transporter gene (*5-HTTLPR*) (adapted from Chiao and Blizinsky 2010). (a) Color map of frequency distribution of IND-COL from Hofstede (2001). (b) Color map of frequency distribution of S alleles of *5-HTTLPR*. (c) Collectivistic nations showed higher prevalence of S allele carriers

Additionally, cultural values and frequency of S allele carriers negatively predicted global prevalence of anxiety and mood disorder. Mediation analyses further indicate that increased frequency of S allele carriers predicted decreased anxiety and mood disorder prevalence due to increased collectivistic cultural values. These findings support the notion that cultural values buffer genetically susceptible populations from increased prevalence of affective disorders and suggest culture–gene coevolution between allelic frequency of 5-HTTLPR and cultural values of individualism–collectivism. A central claim of culture–gene coevolutionary theory is that, once cultural traits are adaptive, it is likely that genetic selection causes refinement of the cognitive and neural architecture responsible for the storage and transmission of those cultural capacities (Boyd and Richerson 1985). An important puzzle for future neuroscience research is to understand how culture–gene coevolution may have shaped mechanisms in the social mind and brain differently across cultural contexts, due to diversity of selection pressures across geographical regions.

2 What Is Cultural Neuroscience?

Here, we examine how theory and methods in cultural neuroscience may prove valuable for investigating how the social brain may have unfolded over the course of culture–gene coevolution. Cultural neuroscience is an emerging research discipline that investigates cultural variation in psychological, neural and genomic processes as a means of articulating the bidirectional relationship of these processes and their emergent properties (Fig. 3) (Chiao and Ambady 2007). Research in cultural neuroscience is motivated by two intriguing questions of human nature:

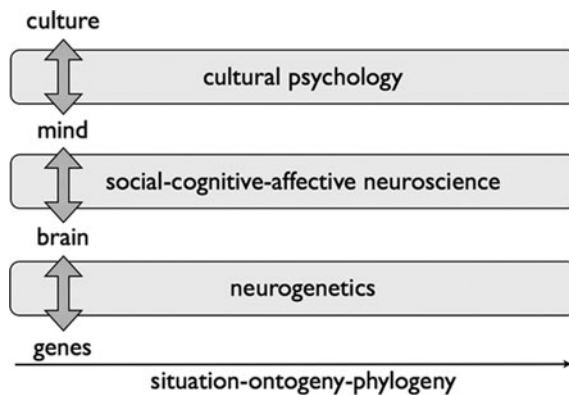


Fig. 3 Illustration of the cultural neuroscience framework, integrating theory from cultural psychology, social/cognitive/affective neuroscience and neurogenetics (adapted from Chiao 2009a, b)

how do cultural traits (e.g., values, beliefs, practices) shape neurobiology (e.g., genetic and neural processes) and behavior, and how do neurobiological mechanisms (e.g., genetic and neural processes) facilitate the emergence and transmission of cultural traits? To address these questions, cultural neuroscientists integrate theory and methods across cultural psychology, neuroscience and neurogenetics (Chiao 2009a, b).

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

Until recently, most behavioral and neuroscience research sampled predominantly from Western, industrialized nations (Henrich et al. 2010; Chiao and Cheon 2010; Fig. 4). Several factors have contributed to the current sampling bias in human neuroscience research. First, human neuroscience research programs typically build either on empirical questions inspired by animal models and case studies of brain damaged patients or on theories from evolutionary psychology. Each of these three starting points for neuroscience research carries implicit assumptions of minimal variability across human populations. Second, human neuroimaging methods have become available only within the past three decades, and are still not available in many non-Western regions of the world. The use of neuroimaging is often prohibitively expensive, making it easier for wealthy, politically stable countries, such as Western industrialized nations, to create the powerful societal infrastructures necessary for novel and timely neuroscientific discovery. Hence, our current state of knowledge of mind–brain mappings to date has largely been restricted to scientific observations made from people living within Western, industrialized nations, leaving a large empirical gap in our understanding of how diverse cultures affect mind, brain and behavior.

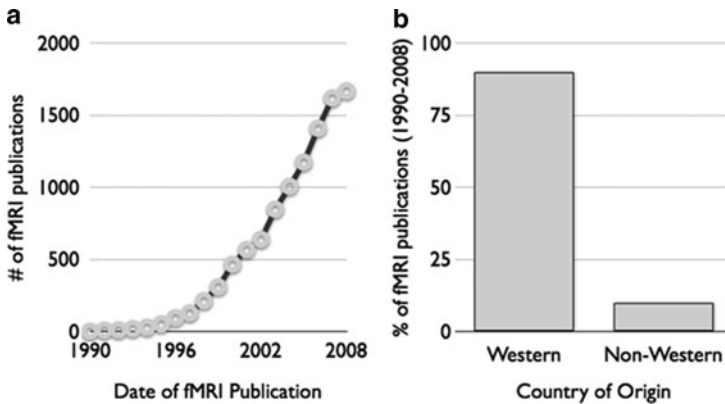


Fig. 4 Growth trends and publication bias in peer-reviewed human neuroimaging literature. (a) Graph illustrating the growth in peer-reviewed human neuroimaging studies from 1990 to 2008. (b) Graph illustrating the publication bias within the human neuroimaging literature whereby the vast majority (~90%) of publications to date originate from a Western country (adapted from Chiao 2009a, b)

3 Cultural Neuroscience of Social Cognition: A Review of the Current Literature

Nevertheless, early efforts by cultural neuroscientists to address the question of how culture influences brain function have proven fruitful, particularly for understanding differences in social cognitive brain processing between Westerners and East Asians (Chiao 2009a). Here, we review recent evidence for cultural influences on social cognitive brain function across a range of domains from self-knowledge and interpersonal perception to empathy and theory of mind (Table 1).

3.1 Self- and Other Knowledge

Cultural values, practices and beliefs shape social behavior in profound ways. One of the most robust ways that values, such as individualism and collectivism, influence human behavior is in self-construal, or how people think about themselves in relation to others. Individualists think of themselves as autonomous from others, while collectivists think of themselves as highly interconnected with others (Markus and Kitayama 1991; Triandis 1995). Recent evidence from social neuroscience indicates that specific brain regions, such as the MPFC and PCC, are involved in self-evaluation and self-knowledge (Amodio and Frith 2006).

Recent cultural neuroscience evidence indicates that neural substrates of self-evaluation are modulated by cultural values of individualism and collectivism. In one study, Caucasians, but not Chinese, showed greater neural activity within the

Table 1 Summary of current evidence for cultural modulation in the neural substrates underlying social cognition

Social cognitive process	Sample	Brain region or waveform	Task	References
Self and others	13 CH	MPFC	Explicit self–other trait judgment	Zhu et al. (2007)
	13 EU			
	20 CA	P3	Oddball detection task	Lewis et al. (2008)
	20 AA			
	14 NR	VMPFC,	Explicit self–other trait judgment	Han et al. (2008)
	14 CHR	DMPFC		
	12 CA	MPFC	Explicit general-contextual self-judgment	Chiao et al. (2009)
	12 JP			
	30 AA	MPFC, PCC	Explicit general-contextual self-judgment	Chiao et al. (2010)
	16 NR	DMPFC,	Explicit self–other trait judgment	Ge et al. (2009)
	16 CHR	VMPFC, PCC		
	14 BUD	DMPFC, VMPFC, ACC	Explicit self–other trait judgment	Han et al. (2008)
	18 US	MPFC, PCC	Explicit self–other trait judgment	Ray et al. (2010)
	47 JP	N400	Word–voice incongruity task	Ishii et al. (2010)
	16 CH	MPFC, ACC	Explicit self–other trait judgment	Wu et al. (2010)
Interpersonal perception	16 TB			
	18 AA	DMPFC, VMPFC	Implicit self–other-trait judgment	Harada et al. (2010)
	14 CA	STS	Reading the mind in the eyes test	Adams et al. (2010)
	14 JP			
	17 CA	Caudate, MPFC	Passive viewing of bodies	Freeman et al. (2009)
Emotion recognition	17 JP			
	18 CA	Amygdala	Passive viewing of faces	Adams et al. (2010)
	16 JP			
	16 CA	Amygdala	Passive viewing of emotional faces	Moriguchi et al. (2005)
	16 JP			
Empathy	10 CA	Amygdala	Explicit emotion recognition	Chiao et al. (2008)
	10 JP			
	24 EA	Amygdala	Explicit emotion recognition	Dertnl et al. (2009)
	24 EU			
	17 CH	ACC	Explicit pain rating	Xu et al. (2009)
Theory-of-mind	16 CA			
	16 US	IFG	False belief task	Kobayashi et al. (2006)
	16 JP			
	12 US	IFG, TPJ	False belief task	Kobayashi et al. (2006)
	12 JP			

ACC anterior cingulate cortex, MPFC medial prefrontal cortex, TPJ temporoparietal junction, P3 late positive potential, VMPFC ventromedial prefrontal cortex, DMPFC dorsomedial prefrontal cortex, PCC posterior cingulate cortex, STS superior temporal sulcus, IFG inferior frontal gyrus, CA Caucasian-American, JP Japanese, EA East Asian, EU European, KO Korean, CH Chinese, NR non-religious, CHR Christian, BUD Buddhist, US American, AA Asian-American, TB Tibetan

MPFC during evaluation of personality traits of one’s self relative to a close other (i.e., mother), suggesting cultural variation in MPFC response during self-evaluation (Zhu et al. 2007; Fig. 5). More recent evidence has demonstrated that cultural values (i.e., individualism–collectivism), rather than cultural affiliation (i.e., East Asian–Westerners) per se, modulate neural response during self-evaluation. In another cross-cultural neuroimaging study, people in both Japan and the USA who endorsed individualistic values show greater MPFC activity for general relative to contextual self-descriptions, whereas people who endorsed collectivistic values show greater MPFC for contextual relative to general self-descriptions (Chiao 2009a). Supporting this view, another study using cultural priming (Hong et al. 2000) showed that even temporarily heightening awareness of individualistic and collectivistic values in bicultural individuals (i.e., bicultural Asian-Americans) modulates MPFC and PCC in a similar manner (Chiao 2009b; Fig. 6). In addition to cultural values modulating neural responses during explicit self processing, a recent neuroimaging study shows that dorsal, but not ventral, regions of MPFC are modulated by cultural priming of individualism and collectivism when thinking about one’s self in an implicit manner (Harada et al. 2010). Such findings suggest that cultural values dynamically shape neural representations during the evaluation,

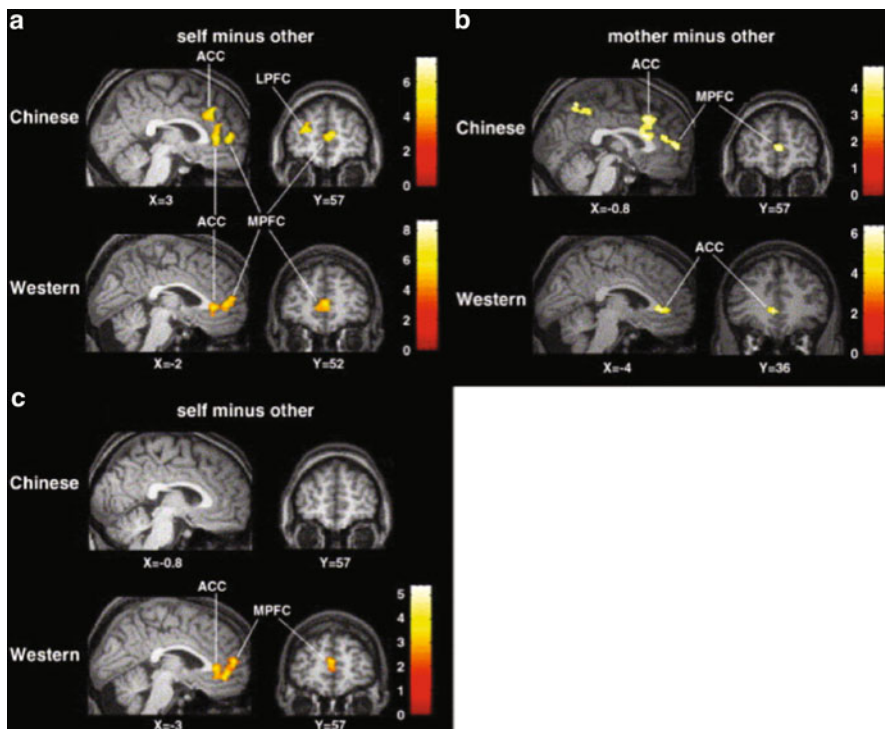


Fig. 5 Brain activations revealed in the contrast between different trait adjective judgment tasks. (a) Self minus other; (b) mother minus other; (c) self minus mother (adapted from Zhu et al. 2007)

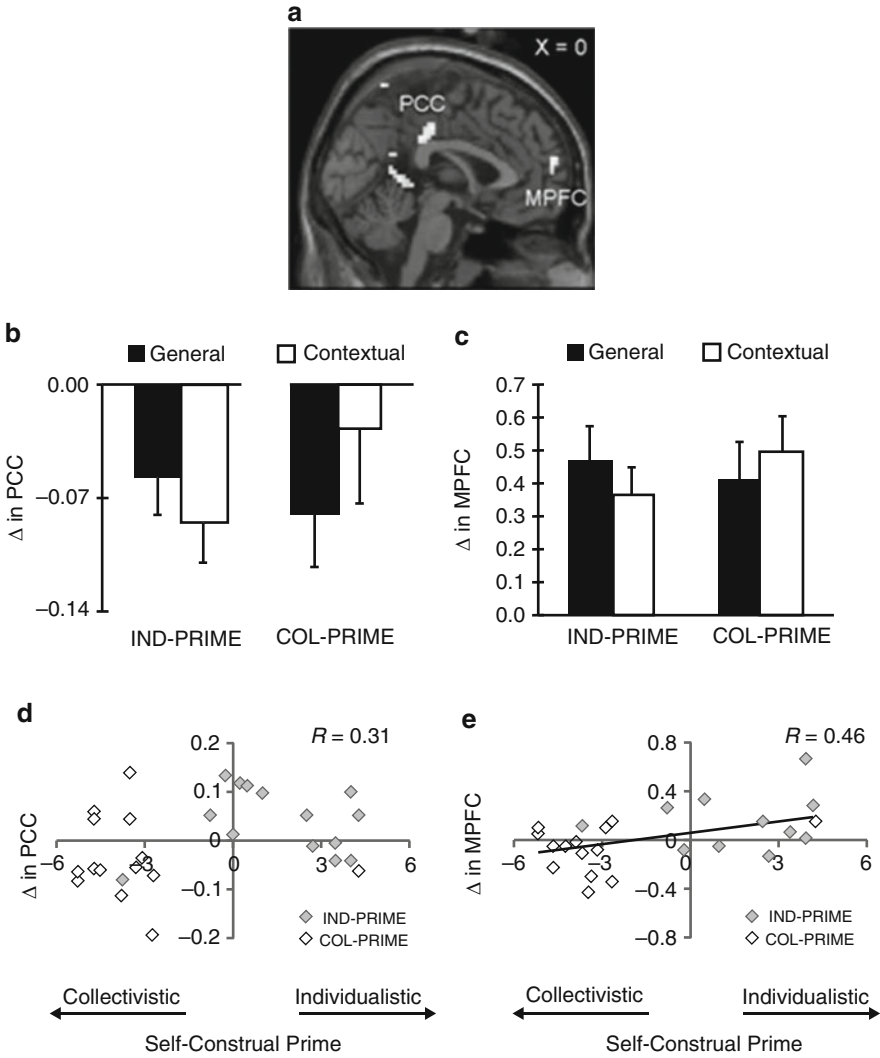


Fig. 6 Dynamic cultural influences on neural representations of self (adapted from Chiao et al. 2010). (a) Modulation of neural activity within cortical midline structures, including the posterior cingulate cortex (PCC) and medial prefrontal cortex (MPFC) as a function of cultural priming. Bicultural participants primed with individualistic cultural values show greater PCC (b) and MPFC (c) to general relative to contextual self-descriptions. Bicultural participants primed with collectivistic cultural values show greater PCC (b) and MPFC (c) response to contextual relative to general self-descriptions. The degree to which a person is primed with individualistic or collectivistic values is positively correlated with neural activity within PCC (d) and MPFC (e) to general relative to contextual self-descriptions, respectively

rather than the detection, of self-relevant information. Taken together, these studies provide convergent evidence that cultural values of individualism–collectivism shape neural representations of both implicit and explicit self-knowledge.

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

Although the lion's share of cultural neuroscience research on knowledge of self and other has been conducted with human neuroimaging methodology, a couple of recent studies have examined the effect of culture on electrophysiological indices of social cognition. In one study, Lewis et al. (2008) measured event-related potentials while participants completed the oddball task, where they are shown visual stimuli in either a frequent or infrequent (i.e., oddball stimulus) manner. Results demonstrated that European-American participants showed greater novelty P3, or late positive potential, amplitude for target events, whereas East Asians showed greater P3 amplitude to oddball events. Another study by Ishii et al. (2010) found that amplitude of the N400, a late negative potential, was significantly larger when individuals perceived incongruent relative to congruent information, and degree of late negativity activity was reliably predicted by chronic social orientation (e.g., interdependence) for females. Both electrophysiological studies demonstrate the effect of cultural values of individualism–collectivism on how people respond to information that is either congruent or incongruent to one another. Hence, cultural values of individualism–collectivism not only affect how people represent knowledge about self and others, but also respond to congruent or incongruent informational cues in the environment.

3.2 *Interpersonal Perception*

Minimal perceptual cues from the body, such as the eye region of the face, convey a wealth of information about what people are thinking and feeling. Recent neuroimaging evidence indicates cultural variation in neural responses when inferring the

internal states of others, particularly from the eye region (Adams et al. 2010). Native Japanese and US Caucasian participants performed the “reading the mind in the eyes” (RME) test, a measure of mental state decoding from visual stimuli only depicting an individual’s eyes (Baron-Cohen et al. 2001). Behaviorally, people were more accurate at decoding the mental state of members of their own culture relative to members of another culture. Neurally, culture was found to also modulate neural activity underlying mental state decoding such that activity in the pSTS increased during the same culture mental state decoding relative to other culture mental state decoding (Fig. 7). This intracultural effect was consistent between the native Japanese and US Caucasian participants, thus excluding any intercultural variation in neural activity. Additionally, the intracultural advantage was significantly negatively correlated with pSTS activity during other culture mental state decoding such that, as pSTS activity increased, the intracultural advantage decreased. This correlation was not significant for same culture mental state decoding from the eyes, suggesting that the intracultural advantage may be due to less pSTS recruitment during other culture mental state decoding. These findings support the universal recruitment of pSTS in ToM, while at the same time revealing culturally modulated pSTS recruitment underlying the intracultural advantage in ToM. Another recent

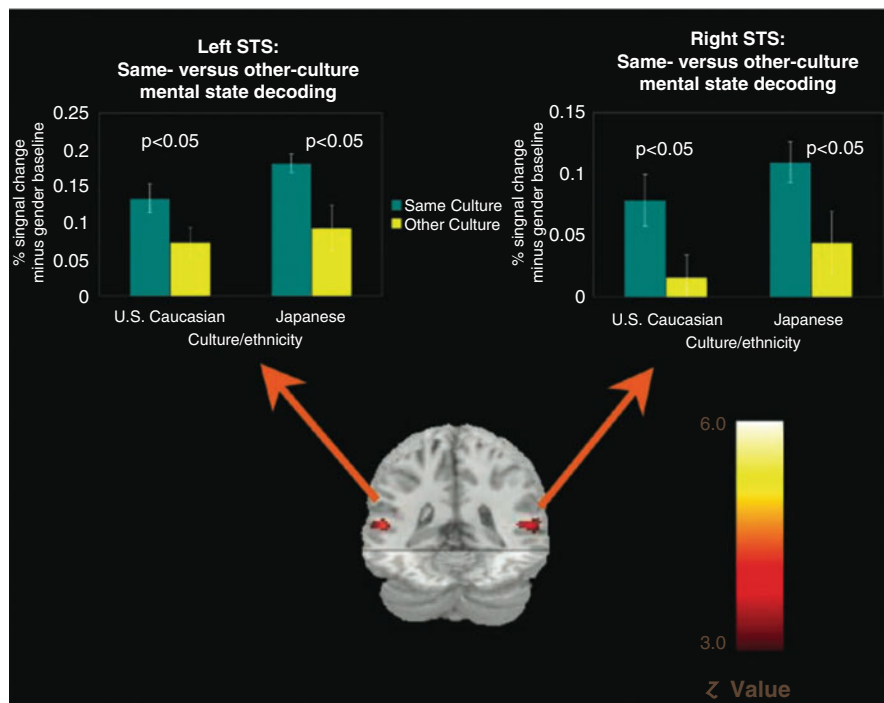


Fig. 7 Graphs depict regions of left and right pSTS activation for same- versus other-culture mental state decoding (RME GD). Results show significantly greater same- versus other-culture activation in both cultural groups for both the left and the right STS (from Adams et al. 2010)

study found that activity within the mesolimbic system responds more to culturally-congruent dominant and submissive facial cues (Freeman et al. 2009). Individuals from egalitarian cultures, such as the USA, show greater mesolimbic response to dominant facial cues whereas individuals from hierarchical cultures, such as Japan, show greater mesolimbic response to submissive facial cues. Taken together, these studies highlight how cultural variation in attribution styles may modulate neural activity underlying processes related to interpersonal perception.

3.3 *Emotion Recognition*

Culture affects how people prefer to experience, express, recognize and regulate their emotions (Mesquita and Leu 2007). East Asian prefer to experience low arousal relative to high arousal positive emotions (Tsai 2007), and are more likely to suppress their emotions relative to Westerners (Butler et al. 2007). Additionally, both East Asians and Westerners demonstrate cultural specificity in emotion recognition, whereby they show greater recognition for emotions expressed by their own cultural group members relative to members of other cultural groups (Elfenbein and Ambady 2002). Recent cultural neuroscience of emotion research has shown cultural specificity effects within a number of brain regions involved in emotion recognition. Moriguchi et al. (2005) found greater activation in the posterior cingulate, supplementary motor cortex and amygdala in Caucasians, relative to Japanese, who showed greater activity within the right inferior frontal, premotor cortex and left insula when participants were asked to explicitly recognize emotions from the face. Chiao et al. (2008) examined neural responses in adults living in either the USA or Japan and found that, across cultures, people exhibit greater bilateral amygdala response to fear faces expressed by their own relative to other culture members (Chiao et al. 2008; Fig. 8). Another recent neuroimaging study comparing neural responses during emotion recognition in Asians and Europeans found a significant negative correlation between duration of stay and amygdala response such that amygdala response during emotion recognition was higher in individuals who were recent immigrants to the region, suggesting that experience alters neural responses to emotional expressions (Dertnl et al. 2009). Taken together, this research indicates that activity within the human amygdala is modulated by cultural group membership. An important question for future research will be to determine whether neural mechanisms that support other facets of emotion, such as experience and regulation, are affected by culture.

3.4 *Empathy*

Empathy is the capacity to share the emotional states of others (Batson et al. 1981; Preston and de Waal 2002). The perception–action model of empathy indicates that empathy is a key motivator (Decety and Grezes 2006) and the proximate

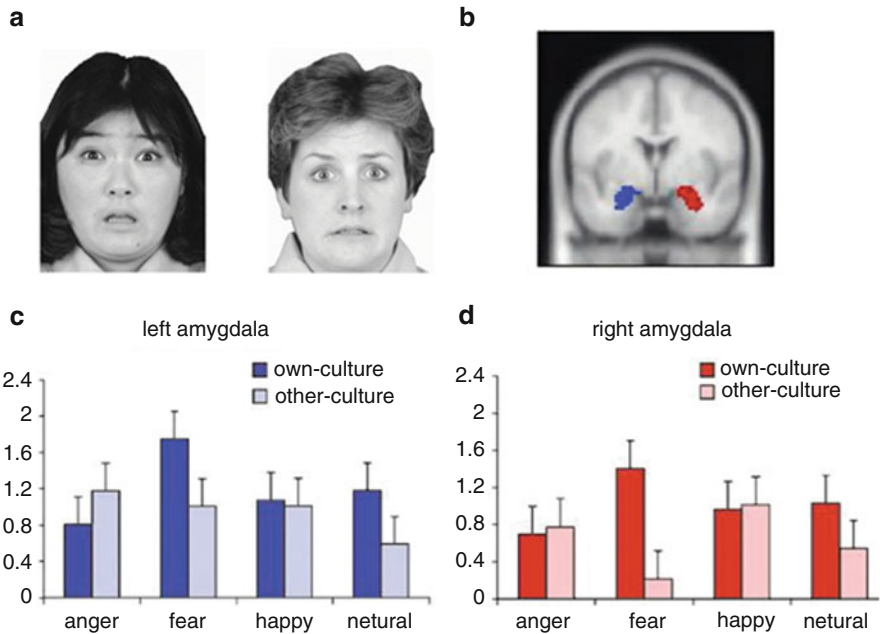


Fig. 8 Cultural specificity in bilateral amygdala response to fear faces (adapted from Chiao et al. 2008). (a) Examples of Japanese and Caucasian-American fear faces. (b) Illustration of bilateral amygdala. Participants show greater left (c) and right (d) amygdala response to fear expressed by members of their own cultural group

mechanism (de Waal 2008) of altruistic behavior, whereby an individual perceives and shares in the distress of another person, and acts to reduce his or her suffering (Preston and de Waal 2002). Prior social neuroscience research indicates that empathy is a multi-component process that includes affect sharing, cognitive perspective taking, and cognitive appraisal (Decety and Jackson 2004; Hein and Singer 2008; Lamm et al. 2007; Olsson and Ochsner 2008). Empathy for pain is supported by neuroanatomical circuits underlying both affective and cognitive processes (Decety and Jackson 2004; Hein and Singer 2008; Lamm et al. 2007; Olsson and Ochsner 2008). A distinct neural matrix, including bilateral AI and ACC (Decety and Jackson 2004; Hein and Singer 2008; Olsson and Ochsner 2008), is thought to underlie the affective components of empathy. AI and ACC code the autonomic and affective dimension of pain and, in particular, the subjective experience of empathy when perceiving pain or distress in others (Decety and Jackson 2004; Hein and Singer 2008; Olsson and Ochsner 2008). A recent neuroimaging study by Xu et al. (2009) examined whether or not cultural group membership modulates neural response during the perception of pain in others. Chinese and Caucasian participants were scanned while observing Chinese and Caucasian targets either in physically painful (e.g., needle stick) or neutral (e.g., Q-tip probe) scenes. All participants showed greater ACC and AI response to painful relative to neutral scenes; however, they also showed greater ACC response to

ingroup relative to outgroup members. These findings demonstrate that cultural group membership affects neural responses to perceived physical pain of others and suggest a neural precursor to group selection in altruistic behavior (Wilson 2006).

3.5 *Theory of Mind*

Another key social cognitive process is theory of mind (ToM), or the ability to understand and represent the psychological state of others (Wellman et al. 2001). Normally developing children demonstrate ToM starting at 4 years of age, while younger children and children with autism typically fail to demonstrate ToM (Baron-Cohen et al. 1985). Such developmental findings provide evidence for ToM as a universal developmental process (Fodor 1983; Scholl and Leslie 1999; Leslie et al. 2004) with an underlying biological basis (Frith and Frith 1999; Scholl and Leslie 1999). While some cross-cultural studies support the universality of ToM, other studies suggest ToM may be culturally and linguistically dependent (for review, see Kobayashi et al. 2006). For example, variation in cultural attribution styles may influence ToM performance in Asian children (Naito 2003) who are raised in a culture that attributes behavior to external and contextual causes rather than to internal causes, as in American/European cultures (Masuda and Nisbett 2001; Nisbett 2003). Similarly, speaking a non-English language with few mental state verbs may negatively influence children's performance on ToM tasks (Vinden 1996).

Neuroimaging evidence provides further evidence for both the universal aspects of (Saxe and Kanwisher 2003; Saxe 2006) and culturally specific influences on ToM processes (Kobayashi et al. 2006). A number of prior neuroimaging studies of theory of mind conducted on individuals from Western populations have found greater activity within the right temporoparietal junction (rTPJ) specifically when participants read stories about another person's thoughts (Saxe and Kanwisher 2003; Saxe 2006). Recently, Kobayashi et al. (2006) used fMRI to examine cultural and linguistic influences on neural activity underlying ToM in American English-speaking monolinguals and Japanese-English late bilinguals. Neural activity was recorded using fMRI while participants completed second-order false-belief ToM stories in both English and Japanese languages. Universally recruited brain regions associated with ToM processing included the right MPFC, right ACC, right MFG/DLPFC, and TPJ. In the American English-speaking monolinguals, culturally modulated neural activity underlying ToM was observed in the right insula, bilateral temporal poles, and right MPFC relative to the Japanese-English bilinguals, while the Japanese-English late bilinguals showed culturally modulated neural activity in the right OFG and right inferior frontal gyrus (IFG) associated with ToM processing relative to the American English-speaking monolinguals. Greater insular and TP activity in the American English-speaking monolinguals suggest that ToM in American culture emphasizes integrating sensory modalities with limbic input, while greater OFG and IFG activity in the Japanese-English late

bilinguals suggest ToM in Japanese culture may rely more on emotional mentalizing. Taken together, these findings demonstrate universality and cultural diversity in neural mechanisms underlying theory of mind.

4 Open Questions for Research on Cultural Neuroscience of Social Cognition

As our review shows, considerable progress has been made in understanding how cultural values, practices and beliefs shape social brain functioning. A network of brain regions, including the amygdala, STS, MPFC, and ACC, display evidence of cultural specificity, whereby neuronal response is heightened when perceiving information or thinking about one's self or others in a culturally-congruent fashion in young adults. However, a number of fundamental questions remain.

One open question for future research is uncovering the trajectory by which cultural specificity in social brain functioning occurs. Are these demonstrations of cortical specialization towards a culturally familiar social percept or cognition are akin to evidence for cortical specialization in language or face perception, whereby neural mechanisms tune to familiar kinds of percepts during development? Akin to language development, do brain structures underlying social cognition tune to culturally specified percepts during certain critical periods early in lifespan? Or does cultural specificity in brain responses occur readily in the absence of developmental input due to cultural and genetic selection of culturally specific neural mechanisms over generations? How does malleability in social brain function in response to cultural context change as a function of aging into late adulthood? Future research is needed to disentangle the malleability of social neural processing as a function of cultural and genetic constraints throughout the lifespan.

Remarkably, cultural neuroscience evidence indicates that the social brain shows sensitivity to cultural frame switching as a function of situational forces. That is, biculturals, who are adept at multiple cultural value systems, can be primed to think of themselves as more individualists or collectivists within a given situation, and such momentary variability in cultural values is reflected in variability in neuronal processing with the social brain. Hence, the process by which cultural and biological mechanisms interact in monocultural and multicultural individuals likely unfolds across macro (e.g., lifespan) and micro (e.g., situation) time scales.

Additionally, future research is needed to better understand the scope of cultural and genetic selection on the human social brain. For instance, in addition to cultural values of individualism–collectivism, what other kinds of cultural values may have been selected for throughout the course of culture–gene coevolution? Cultural psychologist Hofstede (2001) identified four other kinds of cultural value systems that reliably shape human social behavior, including power distance, long-term/short-term orientation, masculinity/femininity and uncertainty avoidance. To the extent that these cultural values, or a subset of them, may have coevolved with

a specific gene or family of genes, it is plausible that neural variation in the social mind and brain may exist due to cultural variation in values and subsequent social behavior.

Perhaps one of the most elusive, yet provocative, avenues for future research in cultural neuroscience of social cognition is acquiring a deeper understanding of the evolutionary function of cultural variation in social brain functioning. That is, uncovering how and when culture shapes social brain function is a laudable and necessary empirical goal as a stepping stone to a larger project of understanding how and why culture–gene coevolution forces shape the human social brain. What kinds of evolutionary selection pressures have led to diversity in cultural value and neurobiological systems? What kinds of evolutionary advantages are afforded to the human species with increased cultural and neural diversity? How might changes in cultural values systems due to immigration and globalization affect the human social brain? How might the human brain construct and constrain human cultural value systems?

The answers to these intriguing questions are finally within our empirical grasp, and there is perhaps no better time for us to learn the answers. As the world becomes increasingly globalized and modern technology facilitates human migration to places and distances with ease and efficiency like never before, deepening our knowledge of how the human brain enables people to adopt and adapt to multiple cultural value systems is critical. Promoting our understanding of how our brains give rise to cultural value systems and vice versa, we gain leverage on what is at stake when we make decisions about how best to achieve optimal co-existence amongst diverse cultural groups. By using the cultural neuroscience framework to identify and investigate candidate phenomena using the multiple levels of analysis approach, we will enhance our chances of understanding how the social brain works across diverse cultural contexts as well as find potential ways to direct this knowledge towards a range of timely public policy issues, such as interethnic ideology and population health, that arise due to our increasingly globalized social interaction.

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