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DATABASES
Entrez Gene: http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=gene
ABCB1 | *BDNF* | *COMT* | CRH | *CRHR1* | CYP1A2 | CYP2C9 | CYP2D6 | CYP3A4 | enolase phosphatase | *FKBP5* | glyoxalase1 | *GNB3* | *GRIK4* | HDAC5 | HSP90 | *HTR1A* | *HTR2A* | *MAOA* | NGFI-A | *SLC6A4* |

FURTHER INFORMATION
Florian Holsboer's homepage: http://www.holsboer.de/
Max Planck Institute of Psychiatry: http://www.mpipsykl.mpg.de/
MARS sample: http://www.MARS-depression.de
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OPINION

Culture-sensitive neural substrates of human cognition: a transcultural neuroimaging approach

Shihui Han and Georg Northoff

Abstract | Our brains and minds are shaped by our experiences, which mainly occur in the context of the culture in which we develop and live. Although psychologists have provided abundant evidence for diversity of human cognition and behaviour across cultures, the question of whether the neural correlates of human cognition are also culture-dependent is often not considered by neuroscientists. However, recent transcultural neuroimaging studies have demonstrated that one's cultural background can influence the neural activity that underlies both high- and low-level cognitive functions. The findings provide a novel approach by which to distinguish culture-sensitive from culture-invariant neural mechanisms of human cognition.

A fascinating mystery facing human beings is how the brain gives rise to the mind. Scientists from various fields are trying to answer this question in different ways and with different viewpoints. On the one hand, neuroscientists focus on finding the fundamental neurophysiological mechanisms of human cognition, which are often implicitly assumed to be universal. On the other hand, cross-cultural psychological research has documented extensive cultural disparity in human cognition, thought and behaviour[1–10] (BOX 1). In this Perspective, we show how the relatively novel approach of transcultural neuroimaging can bridge the gap between neuroscientific investigations of supposedly culture-invariant neural mechanisms and psychological evidence of culture-sensitive cognition.

One way in which psychologists define culture is by examining the facets of which it consists[8]. For example, a 'social culture' is defined by its shared rules of social behaviours and social institutions. Shared ideas and knowledge, such as beliefs and values, in a human group constitute 'subjective culture'. Previous cross-cultural psychological research assessed cultural differences in human cognition mainly by comparing the behavioural performances of Westerners (Europeans and Americans) and East Asians (Chinese, Japanese and Koreans) (BOX 1). Although there is of course no such thing as a homogeneous 'Western' or 'East Asian' culture, Western and East Asian societies differ in many aspects and thus provide good samples for psychologists to investigate cultural differences in human cognition.

What are the roots of transcultural neuroimaging research? Two decades ago, cognitive-neuroscience research that focused mainly on the neural underpinnings of perception, attention, memory, language and emotion did not compare, probably for practical reasons, different cultural groups. In the early 1990s, cognitive-neuroscience research extended into the field of social cognition, targeting the neural correlates of interpersonal and social behaviours. This led to the birth of 'social neuroscience' or 'social cognitive neuroscience' around the turn of the twenty-first century[11–15] (BOX 2). This new field combines mainly cognitive neuroscience and social psychology. As cross-cultural psychology has offered accumulating evidence that social cognition and social behaviour depend greatly on the sociocultural context, social neuroscientists are now beginning to consider cultural effects on the neural substrates of human cognition. Using neuroimaging techniques such as functional MRI (fMRI) and event-related brain potentials (ERPs), researchers have measured neural activity in individuals from different cultural groups who were performing the same cognitive tasks[16–19], or in individuals from one cultural group after they had been primed with different cultural knowledge[20,21] (BOX 3). The meaning of 'cultural differences' could be extended to include not only groups with different social contexts and languages[17,18], but also groups with different religious beliefs[22].

In this Perspective we discuss the accumulating evidence that culture influences the neural mechanisms that underlie both low-level perceptual and attentional processes and high-level social cognition. After reviewing current transcultural neuroimaging studies, we distinguish between the modulatory and constitutional impacts that culture might have on the neural substrates of human cognition. We also discuss the implications of these findings and point out relevant issues for future transcultural neuroimaging investigations.

Box 1 | **Cultural diversity of human cognition**

By comparing cognitive functions in people from Western (European and American) and East Asian (Chinese, Japanese, Korean, *et cetera*) cultures, the 'culture-and-cognition' approach[104] demonstrates that different sociocultural systems give rise to dissimilar thought styles. Westerners generally think in an analytical way, whereas East Asians generally think in a more holistic manner[5,7]. For instance, during a perception task, Americans were better at detecting changes in salient objects than East Asians, and were less affected by contextual information[24,26,27].

Cultural differences are also evident in social cognition. In a game that involved two individuals interacting, Chinese participants were more in tune with their partner's perspective than Americans[105]. Furthermore, Chinese people were more likely to describe memories of social and historical events and focused more on social interactions, whereas European Americans more frequently focused on memories of personal experiences and emphasized their personal roles in events[106]. Westerners were better at remembering trait words that they associated with themselves than they were at remembering words that they associated with people close to them[84,107], whereas Chinese people remembered both equally well[108]. Americans tended to explain behaviours in terms of peoples' dispositions (for example, a person's gender and education), whereas East Asians showed a preference for attributing behaviour to situational factors (for example, environmental events)[9,109] and were more likely to use situational information to predict other people's behaviour[110]. Chinese people endorsed contextual explanations of physical events (for example, friction influencing the movement of an object) more often than Americans, who were more likely to attribute physical events to dispositional factors (for example, an object's weight or composition)[111].

Culture also influences category-based classification of objects: Chinese people organized objects in a more relational (for example, to group a monkey and a banana together because monkeys eat bananas) and less categorical (for example, to group a monkey and a panda together because both are animals) way than European Americans[7,112]. Taken together, these findings provide evidence for the diversity of multiple-level cognitive processes across cultures and the dependence of human cognition on sociocultural contexts.

Cultural effects on cognition

Perceptual processing. It is sometimes assumed that perceptual and attentional mechanisms that have been uncovered in individuals from one cultural group can be applied to people from other cultural groups. However, cross-cultural research has presented evidence for differences in perceptual and attentional processing between European Americans (who are Westerners) and East Asians[6,23]. Specifically, Westerners seem to be inclined to pay more attention to salient objects than to contextual background, whereas East Asians seem to attend more to relations and contexts than to salient objects[24–27]. For instance, Americans have been found to be better at detecting changes in salient objects, whereas Japanese individuals were better at finding changes in contexts[27,28]. Consistent with this, Americans made fewer mistakes when judging the orientation of a rod placed inside a frame (East Asians were more likely to be influenced by the position of the surrounding frame)[24], whereas East Asians could more accurately estimate the relative length of a line within a contextual frame[26].

To assess cultural influences on the neural substrates of perceptual and attentional processes, blood-oxygen-level-dependent (BOLD) signals were measured using fMRI in American and Chinese participants[16]. The participants were asked to rate how pleasant they found various presentations: target objects shown on a white background, background scenes with no discernable target object, and distinct target objects shown against a meaningful background. During the object-only task, Americans showed greater activation in the bilateral middle temporal gyrus, the left superior parietal/angular gyrus and the right superior temporal/supramarginal gyrus than the Chinese participants. The cultural differences were less pronounced in the background-processing task, with American participants showing greater activation in only the left superior occipital cortex (Chinese participants did not show significantly greater activation than Americans in any brain areas). These results suggest that there might be cultural differences in the way that brain regions are engaged during object processing, as brain areas such as the middle temporal cortex are engaged in the retrieval of semantic knowledge during object perception[29]. This idea was further tested in a study that assessed BOLD-response adaptation (that is, the reduction of the BOLD response after repeated exposure to the same stimulus) in brain areas involved in object and background processing in individuals from the United States and Singapore[30]. In both cultural groups, the perception of objects that were placed within background scenes produced adaptation responses bilaterally in the lateral occipital cortex and the parahippocampal gyrus, which are linked, respectively, to object and background processing. However, the adaptation responses in the lateral occipital areas were stronger in the Westerners than in the East Asians, although this cultural difference was evident only in elderly subjects. This suggests that culture-specific experiences of object-focused visual processing play a fundamental part in modulating perceptual processes in the visual cortex and might interact with the effect of age.

Is perceptual processing also affected by the way in which people from different cultures view themselves in relation to their social contexts? Self construal, which is the way in which one understands and explains oneself, plays a key part in social behaviour and is thought to differ between Westerners and East Asians. The Western 'self' seems to be characterized by an independent style that stresses self-focused attention over attention to others, whereas the East Asian self seems to be characterized by an interdependent style that emphasizes the fundamental connections between people in social contexts[2,3]. Does this cultural difference in self construals contribute to the cultural differences in perceptual processing? To investigate this, a recent study[31] used a self-construal priming procedure that is assumed to shift self construals towards either an independent- or an interdependent-self style[32]. Specifically, Chinese participants were primed with independent or interdependent self construals by reading essays that contained either the independent pronoun 'I' or the interdependent pronoun 'we'. The participants were subsequently presented with compound stimuli (that is, large letters composed of small letters[33]) and had to discriminate the global or local properties of the stimuli (that is, they had to identify the large or the small letters, respectively) while their reaction times were recorded. The authors found that interdependent-self priming resulted in faster responses to the global than to the local targets in compound letters, whereas a reverse pattern occurred after independent-self priming[31]. Moreover, a recent ERP study[21] found that priming with independent self construals resulted in an enlarged ERP component (P1) in response to local relative to global targets. The P1 peaked at ~100 ms after the stimulus onset and had maximum amplitudes over the bilateral visual cortex, indicating that it could have arisen in the extrastriate visual cortex[34,35]. By contrast, a reverse pattern (that is, a larger P1 amplitude in response to global versus local targets) was observed after interdependent self-construal priming. These findings suggest that shifting culture-specific self construals might lead to changes of visual perceptual processing in the extrastriate cortex.

Attentional modulation. Cultural differences have also been reported in the attentional network, including in parietal and frontal brain areas. One study[19] used a perceptual judgement task in which attentional control was manipulated using perceptual stimuli. In this task, participants were asked to judge whether the length of a vertical line inside a box matched the length of a previously shown line regardless of the size of the box (a context-independent judgement task that Westerners would be expected to perform better than East Asians), or whether the box–line combination of each stimulus matched the proportional scaling of the preceding combination (a context-dependent judgement task favoured by East Asians)[26]. East Asians showed higher prefrontal and parietal activity during context-independent judgements, whereas Americans showed higher activity in context-dependent judgements (FIG. 1). This suggests that people from both cultures used their attentional network in this task, but that cultural experience affected the magnitude of the neural activity: fewer neural resources were recruited to support attentional modulation in culturally preferred tasks than in non-preferred tasks; this might be similar to the reduced neural activation that arises from task fluency or practice[36].

Language and music. Although some of the brain areas that are activated during language processing, such as the left superior posterior temporal gyrus and the inferior frontal gyrus, are similar for different languages (for example, Chinese, English and Japanese)[37], a number of brain areas are language-specific. For instance, when native English speakers read English words the superior temporal gyrus is activated[37], whereas when native Chinese speakers read Chinese characters the dorsal extent of the inferior parietal lobe is activated[38]. Rather than being an effect of culture in a broad sense, this finding might reflect a basic difference between non-phonetic and phonetic written languages: alphabetic words, such as English words, can be read by assembling fine-grained phonemic units, whereas written Chinese characters consist of intricate strokes and map onto phonology at the mono-syllable level[38]. Interestingly, the differences in the neural correlates of language processing might extend to the processing of non-words. A positron-emission tomography (PET) study of English and Italian students showed that, in English readers, reading non-words induced greatest activation (relative to a resting state) in the left posterior inferior temporal region and in the inferior frontal gyrus. By contrast, reading non-words generated greatest activation (relative to the resting state) in the left temporoparietal junction (TPJ) in Italian readers[39]. These differences probably reflect fundamental differences between the two languages rather than effects of the Italian and English cultures *per se* on language processing.

The finding that there are language-specific neural underpinnings of language processing in healthy participants implies that the neural correlates of language-processing deficits might also differ between individuals from different cultural groups that speak different languages. Indeed, it has been shown that dyslexia, which is a reading problem in people of normal intelligence and schooling, is

Box 2 | **Social neuroscience**

The relatively new field of social neuroscience is the product of the integration of neuroscience (particularly neuroimaging), cognitive science and social sciences (particularly social psychology), and it allows one to investigate the complex and dynamic representation of social interaction in the brain's neural states. The field aims to uncover the neural underpinnings of social processes, such as mental attribution, empathy and moral judgement.

Social neuroscience is inherently cross-disciplinary. For instance, to examine how empathy for pain that someone else is experiencing is modulated by the affective link between individuals, a functional MRI study measured neural responses to perceived pain in confederates who played fairly or unfairly in a game[113]. The authors found that activity in the insular cortex and in the anterior cingulate cortex (ACC) was lower in males when they observed an unfair player receiving pain than when they saw a fair player receiving pain. By contrast, activation in reward-related areas (for example, the nucleus accumbens) was higher in response to pain stimulation applied to the unfair player. Another study assessed whether social exclusion induces 'painful' affective responses (as painful physical stimulation does)[114]. Subjects showed higher ACC activity during a virtual ball-tossing game in which they were ultimately excluded from the game than they showed when they remained included. These studies provide excellent examples of how neuroimaging can be used to estimate the neural underpinnings of complex social interactions.

associated with dysfunction of the left temporoparietal cortex and the left inferior frontal gyrus in English monolinguals[40,41] but with dysfunction of the left middle frontal gyrus in Chinese monolinguals[42]. In addition, relative to healthy controls, English dyslexic children exhibited reduced grey-matter volume in the left parietal region[43], whereas Chinese children with reading problems exhibited reduced grey-matter volume in the left middle frontal gyrus[44]. These results suggest that abnormalities in both functional and anatomical structures of language processing might be language-dependent.

Music processing also shows culture-specific features. The neural substrates of cross-cultural music comprehension have been investigated by scanning American[45] and German[46] musicians while they listened to Western and Chinese music. Both studies found greater lateral frontal activity associated with listening to culturally familiar versus culturally unfamiliar music. In addition, one study reported greater activation of the precentral gyrus and supplementary motor area in response to Western music[46], suggesting that culturally familiar music might be represented in both sensory and motor areas. However, culturally unfamiliar music led to enhanced activity in the right angular gyrus and the middle frontal gyrus, possibly because the processing of unfamiliar music requires higher attentional demands and higher loads on basic auditory processing[46].

A transcultural ERP study investigated whether music experts from different cultures differ in their neural activation in response to culturally familiar and unfamiliar music processes[47]. Recording ERPs from German musicians and Chinese musicians who studied in Germany, the authors measured their response to the perception of short melodic excerpts that were clearly structured into two phrases divided by either a pause (phrased music) or by several notes (unphrased music). They found significant parietal positive activity between 450 and 600 ms after the pause offset for the phrased compared with the unphrased music regardless of the music's style (Chinese or Western) and the subjects' cultural background. However, in an earlier time window (100–450 ms), there was a double dissociation in parietal activity: positive activity between phrased and unphrased music was greater for alien than for familiar melodies, and this effect was stronger in German musicians than in Chinese musicians. Both groups of musicians underwent the same formal training in Western music, consistent with the lack of difference between the groups in terms of their neural activity during the processing of Western music. However, the Chinese musicians had received more exposure to traditional Chinese music than the German musicians. Thus, the ERP results might suggest that a person's experience with a specific culture influences the early stage of their music processing, as indexed by the modulation of the early ERP component.

Box 3 | **Methodological issues in transcultural neuroimaging studies**

Most current transcultural neuroimaging studies have compared people from Western and East Asian cultures. People from North American and European countries are considered to be Western, whereas people from China, Japan or Korea are considered to be East Asian. This raises problems regarding the homogeneity of cultural groups, because there might be country-specific aspects to cultures even within a broad cultural group. The problems become even more significant when considering factors like education and aging that might also interact with the neural substrates of culture-dependent cognitive differences[69,74,115].

Current transcultural neuroimaging research usually uses one functional MRI (fMRI) scanner for the two cultural groups, to avoid data contamination by differences in the scanner magnet. Future research might use two different scanners (of the same make and type) to image cultural groups in their own social context, provided that the scanning environment is otherwise identical. Researchers should also take into account possible effects of culture during data analysis. For example, analyses of fMRI data such as spatial normalization should consider possible differences in brain size and shape in people from different cultures[116], particularly in cross-group comparisons.

Comparing neuroimaging results from two cultural groups can identify effects of 'culture' on the neural substrates of specific cognitive functions. However, as any two cultures differ in many aspects, it cannot attribute the neural differences to specific aspects of the cultures (for example, self construal). Recent research[20,21] has tried to use psychological-priming procedures that might activate specific cultural knowledge in individuals in one cultural group to clarify the contribution of a specific aspect of a culture to culture-specific neural mechanisms of cognitive processes.

Number representation and mental calculation. Arabic numbers are used by various cultural groups for number representation and arithmetic processing. However, the neural mechanisms that underlie mental calculation in these cultures might be different[48]. A recent fMRI study tested this possibility by scanning Chinese people and English-speaking Westerners, all living in China, during number-representation and mental-calculation tasks[17]. In Westerners, judging the orientation of Arabic numeral stimuli generated greater activation in the left supplemental motor area, Broca's area and Wernicke's area (relative to judging the orientation of non-numerical stimuli). By contrast, Chinese participants showed greater activation in the left premotor association area, including Brodmann areas 6, 8 and 9. In addition, Chinese participants showed greater activation in premotor areas during number-addition and number-comparison tasks than during the number-orientation task, whereas Westerners showed increasing activation in the perisylvian area as the task's arithmetic load increased. The lower activation of the left supplemental motor area in Chinese participants relative to Western participants might reflect faster number processing in Chinese people, possibly because the brevity of the Chinese language with respect to numbers might allow for a larger short-term memory[49]. By contrast, English-speaking Westerners activated the language system (Broca's and Wernicke's areas) during mental calculation. This work demonstrates that different language systems might shape the neurocognitive processes of primarily non-language-related functions like mental calculation.

Cultural effects on social cognition

Emotional processes. Behavioural research has shown evidence for cultural influences on emotion processing. For example, both Chinese and Australian children recognised emotions on the faces of people of their own cultural group more accurately than on those of people from another cultural group[50]. These findings support an in-group advantage in emotion recognition[51]. However, whether culture affects the neural mechanisms that underlie emotion processing remains unknown. In a recent fMRI study, native Japanese participants in Japan and Caucasians in the United States were shown photos of Japanese and Caucasian faces expressing fear or non-fearful (for example, angry, happy or neutral) emotions[52]. Fearful faces from the participants' own cultural group induced greater activation in the left and right amygdala than fearful faces from the other culture. Interestingly, this 'cultural

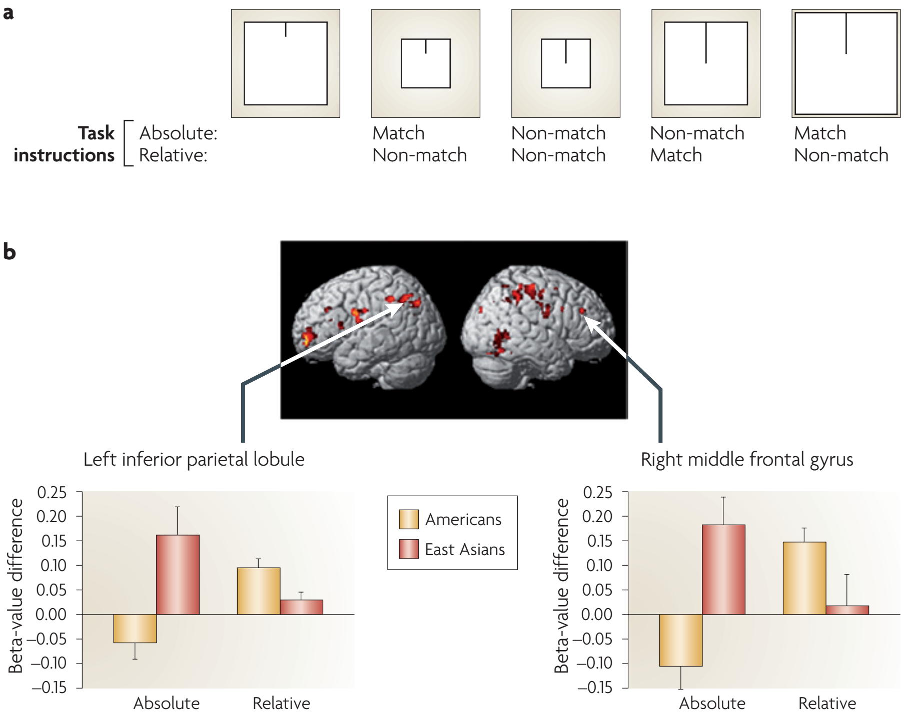

Figure 1 | **Cultural modulation of the neural activity of the attentional network.** **a** | In one study[19], participants had to judge whether the length of a vertical line inside a box matched the length of a previously shown line regardless of the size of the box (a context-independent (absolute) judgement task), or whether the box–line combination of each stimulus matched the proportional scaling of the preceding combination (a context-dependent (relative) judgement task). **b** | Frontoparietal activation associated with judgement tasks in Americans and East Asians. The frontoparietal activity was greater in East Asians (red bars) than in Americans (yellow bars) in the context-independent (absolute) judgement, whereas a reverse pattern was observed in the context-dependent (relative) judgement task. Figure reproduced, with permission, from REF. 19 © (2008) Blackwell Publishing.

tuning' of automatic neural responses was evident only for fearful faces, suggesting that people have heightened arousal to, or vigilance for, fear expressed by members of one's own cultural group.

Mental attribution. One of the fundamental social abilities of humans is the ability to attribute mental states (for example, intentions, desires and beliefs) to others in order to interpret and predict their behaviours[53–55]. The neural basis of this ability, which is referred to as 'theory of mind' (ToM) or 'mentalizing', has been scrutinized by neuroimaging studies since the 1990s[56–61]. Accumulating evidence suggests that a neural circuit consisting of the dorsal medial prefrontal cortex (DMPFC)[56,62–64], the temporal pole[62,63] and the TPJ[65–67] has a key role in mentalizing[68]. Most of these neuroimaging studies were performed in Westerners. To investigate whether the neural bases of mentalizing are influenced by people's cultural background, American-English-speaking monolingual adults and Japanese-English bilingual adults were scanned during a ToM task that involved second-order false-belief stories in the form 'x thinks that y thinks that…' (REF. 69). Relative to judgements of event outcomes that were based on an understanding of physical–causal reasoning, judgements about others' mental states resulted in increased activation in the right DMPFC, the right anterior cingulate cortex (ACC), the right middle frontal gyrus and the dorsal lateral prefrontal cortex in both cultural groups. However, a direct comparison of the groups showed that judgements of mental states produced greater activation in the right insula, the bilateral TPJ and the right DMPFC in monolingual Americans than in bilingual Japanese participants, who showed greater brain activity than the Americans in their right orbital frontal gyrus. These brain areas have been suggested to subserve distinct functions. For example, the insular cortex has been suggested to mediate the connection between the limbic system and frontal regions of the brain[70] and to be involved in the processing of emotion-laden face stimuli[71]. The TPJ might have a role in integrating sensory modalities and limbic inputs[72], and the orbitofrontal gyrus is involved in emotional mentalizing tasks[73]. Thus, it seems that attributing mental states to other people might require the integration of sensory modalities and limbic inputs more for people who grew up in American culture than for people who grew up in Japanese culture, whereas growing up in Japanese culture might result in a particular mental-attribution style that involves 'feeling' others' emotions.

The same research group also compared cultural and linguistic effects on the neural bases of ToM in American-English-speaking monolingual children and Japanese bilingual children aged between 8 and 11 years old[74]. A few brain regions, such as the DMPFC and the precuneus, were recruited in cartoon-based or word-based ToM tasks by both cultural/linguistic groups. However, the word-based ToM task generated greater activity in the left superior temporal sulcus in American than in Japanese children, whereas greater activity was identified in the left inferior temporal gyrus in Japanese than in American children. In addition, stronger activation in the right TPJ in the cartoon-based ToM task was observed in American than in Japanese children. This could be interpreted as being evidence for a weakened self–other distinction in Japanese culture, because the ability to distinguish self from others engages the right TPJ[75,76] and East Asian cultures encourage the use of collectivistic group thinking more than individualistic self thinking to account for human social behaviours[7,77]. In the cartoon-based ToM task, Japanese children showed higher activation in the left anterior superior temporal sulcus and temporal pole than American children. Because the temporal pole has been suggested to integrate sensory information and limbic inputs[72] and to connect past experiences with material that is currently being processed[60], the authors suggested that Japanese children had to integrate sensory and limbic inputs more than American children in the cartoon-based ToM task. Interestingly, the studies discussed above indicate that cultural differences in ToM-related neural activity are not the same in adults and children, suggesting that although children might acquire the ToM ability by the age of 4 to 6 years[60,78,79], acculturation still shapes the underlying neural substrates during later development.

Self representation and self awareness. Given the cultural difference in self construals that have been identified by social psychologists (for example, the independent self in Western cultures and the interdependent self in East Asian cultures)[2,3,80], a recent transcultural neuroimaging study[18] assessed possible cultural modulation of the neural representation of the self using the self-referential task[81]. During this task, subjects have to keep one person (either themselves or someone else) in mind and judge whether a trait adjective (for example, brave or childish) shown on a screen describes that person. The trait-judgement task is usually followed by a memory-retrieval task in which subjects are presented with a list of adjectives and asked to identify whether they have been presented before. Using this paradigm, a number of studies performed in Westerners consistently showed that self-trait judgement induced increased activity in the ventral medial prefrontal cortex (VMPFC) and in the perigenual ACC, relative to judgements of either famous people or otherwise familiar people[82–88]. In addition, VMPFC activity was concomitant with better memory of descriptive traits for the self than for others[18,85] and with subjective ratings of the number of thoughts about the self[89], suggesting a possible role for the VMPFC in coding the self-relatedness of stimuli[90,91]. VMPFC activation linked to self representation was also observed in Chinese participants in the self-referential task[18,22,92]. To assess whether East Asians (who have an interdependent-self style) also use the VMPFC to represent others who are close to them (for example, family members), both English-speaking Westerners and monolingual Chinese subjects in China were scanned in a study[18] that included trait judgement of a close other (the participants' mothers) as well as trait judgement of the self and of a famous person. Whereas self judgement was associated with increased activity in the VMPFC and in the perigenual ACC in both Chinese and Western participants, mother judgement generated increased VMPFC activation only in the Chinese participants (FIG. 2a). This suggests that in Chinese people both the self and one's mother are to be represented in the VMPFC, whereas in Westerners the VMPFC represents only the self. This might provide a neural basis for the different self construals across Western and East Asian cultures[2,3,80].

Culturally distinct neural representations of the self have also been identified in cultural groups that were defined by religious belief[22]. Although some people view belief and religion as the foundation of a culture, in this article we consider (subjective) culture as the larger concept that can be expressed in, among other things, religion. Christianity strongly encourages its believers to surrender to God and to view themselves from God's perspective[93–95]. It could be hypothesized that denying one's self in this way might weaken the VMPFC-mediated encoding of stimuli as self-relevant, whereas emphasizing the evaluation of self-referential stimuli from God's perspective might recruit the DMPFC, activity in which underpins ToM ability[56,62–64].

To test the possible effects of religious belief on the neural activity that is associated with self-referential processing, both non-religious and Christian Chinese participants were scanned while they performed the self-referential task[22]. Self-trait judgement induced increased VMPFC activity in non-religious participants but led to increased DMPFC activity in Christian participants (FIG. 2b). Moreover, the DMPFC activity positively correlated with the extent to which the

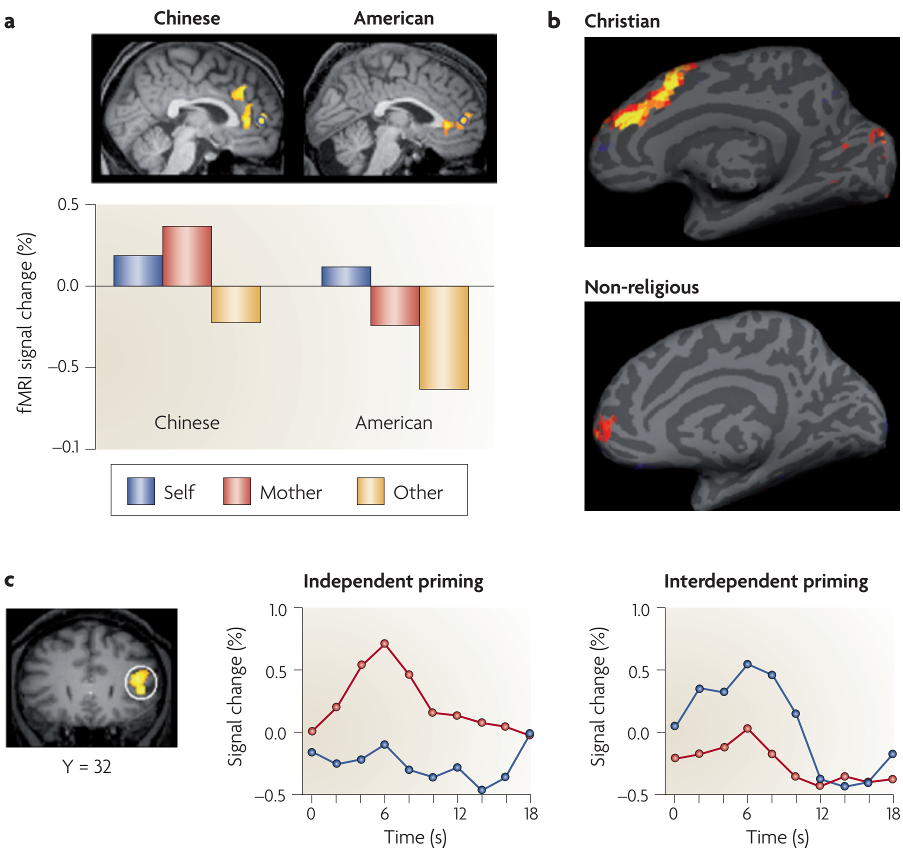

Figure 2 | **Cultural influence on the neural substrates of self representation and self awareness.** **a** | In one study[18], both Chinese people and Westerners conducted trait judgements of themselves, of their mother and of a famous person (an 'other'). The ventral medial prefrontal cortex (VMPFC) and the perigenual ACC (indicated by circles in the scans) showed greater activation in association with self judgement than in association with other judgement in participants from both cultural groups. However, blood-oxygen-level-dependent (BOLD) signal changes in the VMPFC did not differentiate between self and mother judgements in Chinese participants but did differentiate between them in American participants (American participants' signals were greater for self judgement). **b** | In another study[22], both Christian and non-religious participants conducted trait judgements of themselves and a of public person. Christian participants showed higher activation in the dorsal medial prefrontal cortex (DMPFC) for self judgement than for other judgement; non-religious participants showed higher VMPFC activation for self judgement than for other judgement. **c** | In a third study[20], Chinese participants identified the orientation of their own face and the orientations of other, familiar faces in photos after self-construal priming. The scan shows that independent-self-construal priming increased the difference in right frontal cortex activity in response to judging self and familiar faces; the graphs show that BOLD signals differentiated self (red line) and familiar (blue line) faces after independent-self-construal priming (left graph) but did not differ significantly between self and familiar faces after interdependent-self-construal priming (right graph). Part **a** reproduced, with permission, from REF. 18 © (2007) Academic Press. Part **b** reproduced, with permission, from REF. 22 © (2008) Psychology Press. Part **c** reproduced, with permission, from REF. 20 © (2007) Blackwell Publishing.

participants rated the importance of Jesus' opinion in the subjective evaluation of other people's personalities. Because the VMPFC and the DMPFC are thought to be engaged in the representation of stimulus self-relevance (that is, the degree to which a stimulus applies to the self) and the evaluation of self-referential stimuli (that is, the assessment, reappraisal and explicit reasoning of self-related stimuli)[90,91], respectively, the findings suggest that adopting or growing up with Christian beliefs might result in weakened neural encoding of stimulus self-relatedness but might enhance neural activity in areas that mediate the evaluative process that is applied to self-referential stimuli.

The neural substrates of self-awareness — the mental state of understanding that one exists as an individual who is separate from others and who has private thoughts — are thought to include the right frontal cortex both in Westerners[96–98] and in East Asians[99,100], as indicated by the increased activity in this area that results from looking at pictures of one's own face (relative to pictures of others' faces). Although no transcultural neuroimaging research of self-face recognition has been reported, seeing a picture of one's own face might generate greater self awareness in individuals with an independent (that is, Western) self-style than in individuals with an interdependent (that is, East Asian) self-style. To test this hypothesis, Chinese subjects were scanned while they judged the orientation of their own face or those of familiar others in photos[20]. The participants had been primed with independent or interdependent self construals by reading essays that contained either the independent pronoun 'I' or the interdependent pronoun 'we'. Increased right middle frontal activity was observed when the participants interpreted pictures of their own faces (relative to other people's faces), and this activity was enlarged by priming with independent self construals. The increased right frontal activity during self-face judgement after independent self-construal priming was associated with faster behavioural responses to one's own face than to other people's faces (FIG. 2c). These findings indicate that the neural correlates of self awareness that is associated with self-face recognition can be modulated by priming that shifts the self towards independent or interdependent styles. This implies that the differential self awareness during self-face recognition in Westerners and East Asians might be related to their different self construals, an idea that can be tested in future research. Taken together, the findings provide evidence for dynamic and culture-sensitive characteristics in the neural mechanisms that underlie self-referential processing and self awareness.

Conceptual implications

Cultural influences on the neural substrates of human cognition. The aforementioned studies provide strong evidence that the neural mechanisms that underlie cognition might be shaped by a person's sociocultural context. These studies showed, on the one hand, that there are some brain regions in which neural activity is the same across different cultures; for instance, the lateral occipital cortex seems to be implicated in object-processing tasks[30] and the VMPFC in self-referential tasks[18] in individuals from different cultural groups. On the other hand, the neural activity in some brain areas strongly depends on a person's cultural background: for example, that of the premotor cortex during mental calculation[17] and that of the VMPFC during trait judgements of one's mother[18]. In addition, such effects might be consistent with cultural influences on the anatomical structures that are engaged in specific cognitive functions. For example, dyslexic children exhibit culture-specific abnormalities of both function[40–42] and structure[43,44]. Thus, some 'effects of culture' could be due to the use of culturally different task-solving strategies[48] (with concomitant strategy-dependent neural activation patterns), whereas others might be due to changes in the functional (that is, the level of activation) and structural (for example, grey-matter volume) aspects of the neural basis of human cognition. Finally, it is important to remember that even though the same brain region might be recruited by different cultural groups during the same cognitive task, two cultures might have different meanings for the concepts involved in a task. For instance, the fact that the VMPFC is recruited both in Westerners and in Chinese participants during self-trait judgement but is activated by mother-trait judgement in only Chinese participants[18] demonstrates that this region's neural activity depends on the meaning that someone attributes to a psychological concept like the self.

Do cultural experiences only modulate pre-existing and pre-established patterns of neural activity, or do they determine the patterns? In other words, are they modulatory or constitutional? If two different cultural groups differ, for instance, in the activity of a particular brain region during a task (for example, during the attentional task[19]), one might assume that the region's activity is modulated by the cultural difference. By contrast, if culture has a constitutional influence, one's cultural background would determine whether a particular brain region is recruited during a specific task and thus whether that brain region is activated at all. Cultural differences in the meaning of a task, or in the meaning of the concepts used in a task, might result in constitutional effects of culture on neural activation. The frequent use of particular task-solving strategies by people from different cultures might result in both modulatory and constitutional effects of culture.

The current results indicate that some brain regions' neural activities might merely be modulated by cultural differences, whereas others' recruitment might depend constitutionally on the cultural context. If brain regions and their connectivity (for example, their wiring) are constitutionally dependent on the environmental context, it would be impossible to consider the brain in isolation from the environment — one might consequently speak of what has been called an 'embedded brain' (REF. 101).

Nature and nurture. Cultural neuroscience is ideally suited to tackle the long-standing question regarding the extent to which a person's brain function is determined by their genetic background (nature) and by their experiences (nurture). Future transcultural neuroimaging studies could investigate alleles that do or do not differ between cultural groups and then relate their findings to the neural activity that is associated with culture-invariant and culture-sensitive tasks and stimuli. Although this will require complex designs, such investigations might contribute to a better understanding of the interaction between genetic and environmental factors. Studying second-generation immigrants would provide a way to investigate the interaction between genetic and cultural backgrounds. It would also be interesting to study whether differences in responses to pharmacological drugs between ethnicities ('ethnopharmacology' (REFS 102,103)) are due to genetics or to culture-sensitive neural mechanisms. Findings from this area might contribute to the development of specific, and thus improved, psychopharmacological treatment across cultures.

Conclusions and future directions

Although transcultural neuroimaging studies indicate that culture shapes the functional anatomy of multiple-level cognitive functions, they also raise interesting and important questions for future research. For example, how do culture-sensitive and culture-invariant neural substrates contribute to cognition and behaviour? Future research could also examine how specific aspects of culture, such as self styles or beliefs, affect the neural mechanisms of human cognition. Furthermore, it will be interesting to determine whether culture influences both the functional and the structural neural bases of human cognition, and whether effects of culture are constitutional and/or modulatory.

In addition to these basic questions, it will be interesting to investigate how cultural influences on the neural substrates of human cognition interact with the effects of development and aging. Another important question is whether and how the brain adapts to living in a new culture: what are the neural differences between native people and newly arrived, short-term and long-term immigrants? fMRI studies of immigrants might help us to understand where, how and on what timescale the neural substrates of cognitive processes change as a function of cultural influence. Cultural sensitivity might also depend on the period in which one moves from one culture to another. Moving from one culture to another during a time of high neural plasticity, such as adolescence or early childhood, might have greater effects on neural activity than changing cultures in adulthood.

Another interesting question is whether there are culture-specific symptoms of psychiatric disorders like schizophrenia and depression and, if so, whether these are reflected in structural or functional neural differences. For example, the specific form of delusion that is experienced by a patient with schizophrenia might depend on the patient's cultural background (for example, the feeling of being manipulated by a sensor in one's brain versus the feeling of being Jesus or some other religious figure). If this is indeed the case, then neuronal abnormalities in psychiatric disorders might be at least partially culture-specific, and this in turn might influence diagnosis and therapy.

We have discussed how transcultural neuroimaging allows us to identify culture-invariant and culture-sensitive neural substrates of human cognition. Transcultural neuroimaging is based on social psychology and cognitive neuroscience and bridges the gap between the two disciplines. Recent studies demonstrated that groups that come from different cultures or that have been exposed to culturally different stimuli have differences in neural activity. As this is true for both high-level cognition (for example, social cognition) and low-level cognition (for example, perception), we assume that our brain's activity is strongly and, at least in part, constitutionally shaped by its sociocultural context. We conclude that by revealing the dependence of neural activity on sociocultural contexts, the novel field of transcultural neuroimaging might provide new insight into the human brain and its unique principles of neural plasticity.

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FURTHER INFORMATION

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