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to salient objects than to contextual back-ground, 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 frame²⁶.

To assess cultural influences on the neural substrates of perceptual and attentional processes, blood-oxygen-level-

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 study³¹ used a self-construal priming procedure that is assumed to shift self construals towards either an independent- or an interdependent-self style³². 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 letters³³) 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 priming³¹. Moreover, a recent ERP study21 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 study19 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 contextindependent 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 contextdependent 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 practice³⁶.

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 activated³⁷. whereas when native Chinese speakers read Chinese characters the dorsal extent of the inferior parietal lobe is activated³⁸. 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 level³⁸. Interestingly, the differences in the neural correlates of language processing might extend to the processing of non-words. A positronemission 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 readers39. These differences probably reflect fundamental differences between the two languages rather than effects of the Italian and English cultures per e on language processing.

The finding that there are languagespecific neural underpinnings of language processing in healthy participants implies that the neural correlates of languageprocessing deficits might also differ between individuals from different cultural groups that speak different languages. (a) 15(i) 15(a) 5(i) 15(a) 33901 Tm(i) 15(i) 15(i) 15(i) 15(i) 37(s) 15(t) 3.

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 game¹¹³. 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-toss(g)15()37(a) [1]8.2 0 0 J8.2 0 0 J5()37(s)15(i)15(h)15(o)1516(d7(o)15(n)1r)32(e)15

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 monolinguals⁴². In addition, relative to healthy controls, English dyslexic children exhibited reduced grey-matter volume in the left parietal region⁴³, whereas Chinese children with reading problems exhibited reduced grey-matter volume in the left middle frontal gyrus⁴⁴. These results suggest that abnormalities in both functional and anatomical structures of language processing might be language-dependent.

Music processing also shows culturespecific features. The neural substrates of cross-cultural music comprehension have been investigated by scanning American⁴⁵ and German⁴⁶ musicians while they listened to Western and Chinese music. Both studies

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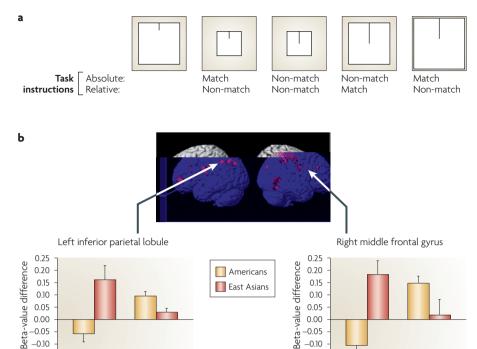


Figure 1 | \mathbf{C} | In one study spatial participants had to judge whether the length of a vertical line inside a box matched the length of a previously shown line regardless of the size of the box (a context-independent (absolute) judgement task), or whether the box-line combination of each stimulus matched the proportional scaling of the preceding combination (a context-dependent (relative) judgement task). | 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.

-0.15

Absolute

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.

-0.15

Absolute

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 1990s⁵⁶⁻⁶¹. 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 mentalizing⁶⁸. 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-Englishspeaking monolingual adults and Japanese-English bilingual adults were scanned during

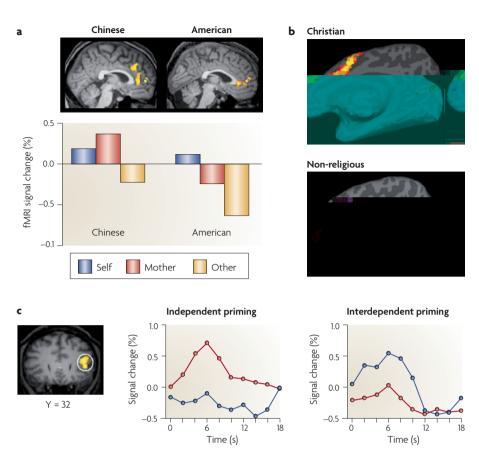
a ToM task that involved second-order false-belief stories in the form 'x thinks that y thinks that...' (REF. 69). Relative to judgements of event outcomes that were based on an understanding of physical-causal reasoning, judgements about others' mental states resulted in increased activation in the 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 brain⁷⁰ and to be involved in the processing of emotionladen face stimuli71. The TPJ might have a role in integrating sensory modalities and

limbic inputs⁷², and the orbitofrontal gyrus is involved in emotional mentalizing tasks⁷³. 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 old74. 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 cartoonbased 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 inputs⁷² and to connect past experiences with material that is currently being processed⁶⁰, 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 task⁸¹. 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 self⁸⁹, 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 study18 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 belief²². Although some people view belief and religion as the foundation of a culture, in this article we consider (subjective) culture



 \dots \dots \dots \dots \dots In one study¹⁸, 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). In another study²², 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. In a third study²⁰, 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 independentself-construal priming (left graph) but did not differ significantly between self and familiar faces after interdependent-self-construal priming (right graph). Part reproduced, with permission, from REF. 18 © (2007) Academic Press, Part reproduced, with permission, from REF. 22 © (2008) Psychology Press, Part, reproduced, with permission, from REF. 20 © (2007) Blackwell Publishing.

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 task²². 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

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 selfreferential stimuli (that is, the assessment, reappraisal and explicit reasoning of selfrelated 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 Asians99,100, 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 selfface 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 photos²⁰. 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 selfconstrual 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 tasks³⁰ and the VMPFC in self-referential tasks¹⁸ 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 calculation¹⁷ and that of the VMPFC during trait judgements of one's mother¹⁸. 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 strategies⁴⁸ (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 participants¹⁸ 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 task¹⁹),

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

tive 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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> > doi:10.1038/nrn2456

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