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Opinion

A Culture–Behavior–Brain Loop Model of Human Development

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Increasing evidence suggests that cultural influences on brain activity are associated with multiple cognitive and affective processes. These findings prompt an integrative framework to account for dynamic interactions between culture, behavior, and the brain. We put forward a culture–behavior–brain (CBB) loop model of human development that proposes that culture shapes the brain by contextualizing behavior, and the brain fits and modifies culture via behavioral influences. Genes provide a fundamental basis for, and interact with, the CBB loop at both individual and population levels. The CBB loop model advances our understanding of the dynamic relationships between culture, behavior, and the brain, which are crucial for human phylogeny and ontogeny. Future brain changes due to cultural influences are discussed based on the CBB loop model.

Trends

Cultural neuroscience research combines cultural psychology, brain imaging, and genetics to investigate whether and how cultural contexts/experiences interact with genes to shape the functional organization of human brain and behavior.

Cultural neuroscience findings suggest indirect culture–brain interactions, through practice of behaviors, and direct culture–brain interactions, which constitute an interacting loop that provides a basis of human development.

The CBB loop model of human development considers different timescales along which genes and culture interact with the brain and behavior, and highlights genetic interactions with the CBB loop.

The CBB loop model can be used to predict future brain changes.

Neuroscience Enters the Culture Arena

Why do people in culturally-distinct societies behave differently? This fascinating question has been studied extensively in psychology by examining human cognitive and affective processes across **cultures** [1,2]. For example, one line of research that compares individuals from East Asian and Western cultures has revealed that East Asians tend to attend to contexts and relationships between objects [3,4], categorize objects in terms of their relationships [5], emphasize contextual effects during causal attribution of physical and social events [6,7], view the self as being interdependent with significant others and social contexts [8,9], and prefer low-arousal positive affective states [10]. By contrast, individuals from Western cultures are inclined to attend to a focal object, categorize objects by their internal attributes, emphasize individuals' internal dispositions during causal judgments, view the self as being independent of others and social contexts, and favor high-arousal positive affective states. These findings support a conceptual framework that **collectivistic** East Asian cultures foster a holistic thinking style whereas **individualistic** Western cultures cultivate an analytic thinking style [11].

Because mental activity is underpinned by the neurobiology of the brain that is shaped by experience [12], increasing interest has emerged in the discovery of brain activities that underlie cultural differences in mental processes and behaviors. Viewing culture as beliefs and behavioral scripts that are shared by a group of individuals and constitute social environments [13], cultural neuroscience combines cultural psychology and neurophysiological measures [e.g., **functional magnetic resonance imaging** (fMRI) and **event-related potentials** (ERPs), see Glossary] to investigate whether and how cultural contexts/experiences shape the functional organization of the human brain and to what degree culturally-distinct patterns of behavior are linked to different neural correlates across cultures [13–19]. Recent studies have revealed numerous differences in brain responses between individuals from East Asian and Western cultures in association with

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 http://dx.doi.org/10.1016/j.tics.2015.08.010

visual perception [20–22], attention [23,24], causal attribution [25], processing semantic relationships [26], processing music [27,28], mental calculation [29], self-face recognition [30,31], self-reflection [32–36], perception of body gesture [37], mental state reasoning [38,39], empathy [40,41], and trait inference [42] (Box 1). Researchers have also investigated the role of a specific cultural trait in mediating individual differences [33,35] and cultural group differences in brain activities [24,36,42]. Studies of **cultural priming** (Box 1) have shown that reminding participants in laboratory studies of specific East Asian/Western cultural values, such as independence versus interdependence, modulates brain activity during tasks that engage pain perception [43], visual perception [44], self-face recognition [45], self-reflection [46–48], motor processing [49], and brain activity during a resting state [50].

The increasing number of cultural neuroscience findings propels a conceptual framework that integrates dynamic interactions between culture and the brain to elucidate (i) how culture shapes the brain by contextualizing behavior, and (ii) how the brain modifies culture via behavioral influences. Such a framework is important for understanding how genes and culture shape the brain during long-term **gene–culture coevolution** and during lifespan **gene × culture interactions**. There have been profound discussions of the interactions between sociocultural contexts, genes, and culture–gene coevolution [51–54], and between a cultural community and its individuals [55]. These insightful discussions suggest a framework that locates culture in a circular interaction (or a loop) with other factors to explain sociocultural and genetic influences on human development from a macroscopic perspective [51,52]. The current paper proposes a CBB loop model of human development and considers empirical findings related to the interactions between different parts of the CBB loop. The CBB loop model distinguishes between culturally contextualized and culturally voluntary behaviors and clarifies behavior-mediated and direct culture–brain interactions. The CBB loop model also provides a new perspective on the relationship between genes and the interacting CBB loop during human development by highlighting the differential effects of culture and gene on brain and behavior. Together, the CBB loop model aims to complement the previous macromodel of human development [51,52] by elucidating idiographic relationships between culture, behavior, and the brain.

Box 1. Cultural Neuroscience Findings

Cultural neuroscience aims to account for cultural differences in behavior by inspecting culture-specific and culture-universal neural activity underlying cognitive and affective processes. Most cross-cultural brain imaging studies focus on the comparison between individuals from East Asian and Western cultures and their culture-specific patterns of brain activity. Cultural neuroscience research also investigates whether observed cultural group differences in brain activity are mediated by specific cultural values. Cultural priming studies, based on the idea that an individual may have multiple cultural systems, and is able to switch between different cultural systems in response to specific social contexts and interactions, investigate whether and how brain activity involved in a specific task varies as a consequence of recent access to specific cultural values and beliefs. Consistent findings of cross-cultural and cultural priming studies help to establish causal relationships between culture and brain function.

Cultural neuroscience studies cover a wide range of topics from low-level sensory/perceptual processing to high-level social cognitive and affective processing. An increasing number of cultural neuroscience studies allow meta-analysis of published studies to examine convergent differences in brain activity between East Asian and Western cultures. A quantitative meta-analysis of 35 functional MRI studies [106] revealed that social cognitive processes including self-reflection, mentalizing, and moral judgment are associated with stronger activity in the dorsal medial prefrontal cortex, lateral frontal cortex, and temporoparietal junction in East Asians, but with stronger activity in the anterior cingulate, ventral medial prefrontal cortex, and bilateral insula in Westerners. Social affective processes related to empathy, emotion recognition, and reward are associated with stronger activity in the right dorsal lateral frontal cortex in East Asians, but with greater activity in the left insula and right temporal pole in Westerners. Non-social processes including visual spatial or object processing, visual attention, arithmetic, and causal judgments on physical events induce stronger activity in the left inferior parietal cortex, left middle occipital, and left superior parietal cortex in East Asians, but greater activations in the right lingual gyrus, right inferior parietal cortex, and precuneus in Westerners. These findings implicate that East Asian/Western cultures exhibit influences on multiple brain regions that are engaged in cognitive and affective processes. East Asian cultures are characterized by increased neural activity related to mentalizing others and emotion regulation, whereas Western cultures are characterized with enhanced neural activity underlying self-relevance encoding and emotional reactivity.

Glossary

Collectivism: a basic cultural element that emphasizes close links among individuals who view themselves primarily as parts of a whole such as a family, a social group, or a nation. People in collectivistic culture are mainly motivated by the norms and duties imposed by the collective entity and are constrained by social relationships with others.

Culture: beliefs/values/norms and behavioral scripts shared by a group of individuals, which together constitute a social environment in which individuals of a social group develop and evolve.

Cultural priming: an experimental procedure that shifts individual mindsets toward one or another set of cultural beliefs/values by asking participants to read essays or view pictures containing specific cultural elements.

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

Functional magnetic resonance imaging (fMRI): a noninvasive method for recording blood oxygenation level-dependent signals that have high spatial resolution and are used to examine brain responses associated with specific stimuli or tasks.

Gene–culture coevolution: a model of human evolution that assumes that genes and culture are two inheritance systems that evolve through similar mechanisms such as mutation and drift. Culture does have novel selection mechanisms in that individuals and groups can to some extent choose among cultural variants to adopt. People can also invent new traits in non-random ways. Hence, cultural evolution is inherently faster than genetic evolution. Cultural traits evolve and influence the social and physical environments under which genetic selection operates [53,54].

Gene × culture interaction: a model that posits that culture-specific behaviors are influenced by individual genetic makeup. This model concerns culturally moderated associations between specific genes and behavioral/psychological tendencies [90].

The CBB Loop Model of Human Development

The CBB Loop Model

The CBB loop model, as illustrated in Figure 1, posits that novel ideas are created by individuals and are diffuse in a population through social interactions in a specific ecological environment to become dominant shared beliefs and behavioral scripts that influence and contextualize human behavior. The functional and/or structural organization of the brain, owing to its inherent plasticity, changes as a consequence of absorbing cultural values and performing culturally patterned behaviors. The modified brain then guides individual behavior to fit into specific cultural contexts, and also modifies concurrent sociocultural environments. The CBB loop model proposes two types of behaviors. Culturally contextualized behavior (CC-behavior) refers to overt actions that are mainly governed by a specific cultural context, such as when a Chinese student who is accustomed to accepting a professor's opinion in China arrives in the USA and imitates American students to argue with a professor. CC-behavior may not occur when leaving a specific cultural environment. Culturally voluntary behavior (CV-behavior) denotes overt actions that are guided by specific cultural beliefs/values and behavioral scripts that are encouraged by a specific cultural environment and are embedded in the brain. For example, after the Chinese student has studied in the USA for a long time, and has internalized Western cultural values such as independence, he may default to arguing with a professor, regardless of the actions of his peers. CV-behaviors can occur independently of a specific cultural context if the cultural system in the brain remains stable to some degree.

The CBB loop model also distinguishes between two types of culture–brain interactions. Behavior-mediated culture–brain interaction refers to the interplay between culture and brain via overt behavioral practice. For instance, Western cultural values such as independence in the USA encourage the Chinese student to argue with his professors, and practicing such behaviors influences his brain. Direct culture–brain interaction refers to the interplay between culture and brain that does not involve overt actions. For example, reminding individuals of specific cultural values such as independence or interdependence in a laboratory setting can directly modulate brain activity. Thus, in the CBB loop model, behavior is not simply considered as a consequence of culture–brain interaction. Instead, behavior is considered as a part of the mechanisms of human development. The three key nodes, culture, behavior, and the brain, dynamically interact through their mutual connections and constitute a loop. Each node, and the connection

Individualism: a basic cultural element that emphasizes the importance of independence, one's own goals/preferences, needs/desires, and rights in thought and behavior. People in an individualistic culture give priority to personal rather than to group goals.

Independent self-construal: the cultural trait of viewing the self as autonomous and bounded entity, emphasizing independence and uniqueness of the self.

Interdependent self-construal: the cultural trait of viewing the self as interconnected and overlapping with close others, emphasizing harmony with close others.

Medial prefrontal cortex (mPFC): the medial region of the prefrontal cortex that is involved in social cognition, with the dorsal part being engaged in mental state reasoning and the ventral part engaged in self-reflection.

Temporoparietal junction (TPJ): a brain region at the border of the posterior parts of the temporal lobe and the inferior parts of the parietal lobe. This brain region is engaged in taking the perspective of others and inferring their mental states.

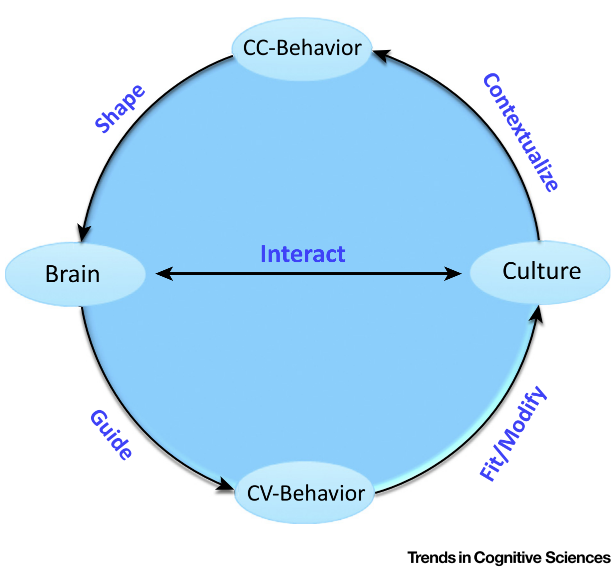


Figure 1. Illustration of the CBB Loop Model of Human Development. Cultural environments contextualize human behaviors. Learning novel cultural beliefs and the practice of different behavioral scripts in turn modify the functional organization of the brain. The modified brain then guides individual behavior to voluntarily fit into a cultural context and meanwhile to modify current cultural environments. Direct interactions also occur between culture and brain without overt behavior. Abbreviations: CBB, culture–behavior–brain, CC-Behavior, culturally contextualized behavior; CV-Behavior, culturally voluntary behavior.

between two nodes of the CBB loop, vary continuously across time and influence human phylogeny and ontogeny.

To illustrate human development in the CBB loop framework, let us consider a key cultural trait (i.e., interdependence/independence) that differentiates between East Asian and Western societies (Western culture encourages **independent self-construal** that views the self as an autonomous and bounded entity, whereas East Asian culture promotes **interdependent self-construal** that views the self as interconnected and overlapping with close others [8]). Previous research suggests that the idea of interdependence/independence emerged during dynamic changes of ecological environments (e.g., adaptation to rural environments prioritizes social obligation/duty and social belonging to promote a strong connection between the self and others, whereas adaptation to urban environments prioritizes choice and personal possessions to foster the unique self [56]) and during specific social practice (e.g., farming and fishing communities emphasize harmonious social interdependence, whereas herding communities emphasize individual decision-making and foster social independence [57]). Individuals dominated by interdependence or independence behave differently, such as categorizing objects in terms of their relationships or attributes, respectively [5,8]. Moreover, priming interdependence or independence in laboratories induces behavioral changes. For instance, priming interdependence speeds responses to a friend's face, whereas priming independence speeds responses to one's own face [45]). Cultural neuroscience research has further revealed that interdependence/independence correspond to distinct patterns of brain activity in different cultures, such as increased activity in the **temporoparietal junction** (TPJ) in East Asians compared to Westerns [36] (Box 1). Moreover, priming interdependence/independence can lead to changes of brain activity. Specifically, priming independence increases right frontal activity during perception of one's own face [45–50]. Culturally patterned brain activity, such as the increased TPJ activity in East Asians [36], may be associated with the ability to take others' perspectives voluntarily [58] such that one can easily fit into a collectivistic cultural context. Therefore, interdependence/independence, behavior, and related brain function constitute a circular interaction during which culture, behavior, and the brain vary dynamically.

At the group level, behaviors guided by shared beliefs may lead to similar changes of brain functional organization in a population, and this facilitates group behavioral adaptation to sociocultural contexts. In support of this notion, cultural neuroscience studies have shown evidence for cultural group differences in brain activity and behavior (e.g., Westerners vs East Asians [20–32], atheists vs Christians/Buddhists [33,34]). However, the group difference does not necessarily indicate homogeneity of brain activity and behavior across all individuals in a society. At the individual level, practice of culture-specific behavioral scripts results in unique functional organization of the brain and associations between a cultural trait and brain activity {e.g., correlations between interdependence and activity in the **medial prefrontal cortex** (mPFC) across individuals [35,36]} that can provide a neural basis of CV-behavior and help an individual to adapt to a cultural context. This occurs during both child development in a specific sociocultural environment and adult acculturation during emigration. Human development is influenced by how easily each node of the CBB loop can be modified and changed, how strongly two connective nodes influence each other, and how quickly a circular interaction in the CBB loop occurs. The CBB loop model characterizes dynamic interactions between culture, behavior, and the brain by assuming culture-induced brain changes in a population during human phylogeny, and in an individual during human ontogeny. Next we will discuss evidence for connections between each pairing of nodes in the CBB loop.

Culture Influences Behavior

The impact of culture on behavior is evident in both the history of humankind and in extant societies. Shared cultural beliefs can induce huge behavioral changes. For instance, shared beliefs that farming would supply more food produced one motivation for transition from gathering/hunting to farming during the Agricultural Revolution [59]. There are many behavioral differences in contemporary individualism/collectivism societies that developed as adaptations to the environment [60]. As an example, at the individual level, parents who believe/value independence in an individualistic society may put their children to sleep in separate bedrooms after birth, whereas parents who believe/value interdependence in a collectivistic society may share a bedroom with their children until early adulthood [61]. There are ample evidence that people acquire different beliefs and behavioral scripts that lead to culturally-distinct behaviors [62]. Cultural priming studies in laboratories provide direct evidence for influences of cultural beliefs/values on behavior. For example, priming East Asian or Western cultural values altered behavioral performance during tasks that required causal attribution [63], face recognition [45], memory recall [64], etc. Thus cultural influences on behavior are evident in both daily life and laboratory observations.

Behavioral Practices Induce Brain Changes

The intrinsic nature of plasticity allows the brain to change in structure and function in response to both the environment and individual experience [65]. Brain imaging research has demonstrated unique structural/functional variations of the brains of musicians [66], taxi drivers [67], and jugglers [68] owing to their long-term behavioral practices. Interpersonal interactions between close individuals in a collectivistic culture are associated with overlapping neural representations of oneself and close others in the mPFC, whereas practices of independent behavior in an individualistic culture are associated with separate neural representations of the self and close others [32]. Greater activity in the cingulate cortex in response to perceived pain in racial in-group versus out-group members can be reduced after daily interactions with racial out-group individuals [69–71]. These findings indicate that the functional and structural organization of the brain is highly sensitive to culturally contextualized behavior and life experience.

Culture Influences the Brain

Recent cultural neuroscience studies have shown ample empirical evidence for the interaction between culture and the brain. The cross-cultural brain-imaging approach that compared brain activities of individuals from different cultural groups has revealed cultural group differences in brain activity during multiple cognitive and affective processes. For example, Westerners showed greater mPFC activity during self-reflection, whereas Chinese showed greater TPJ activity during self-reflection [36] (Box 1). Cultural group differences in brain activity were also observed in individuals with or without religious beliefs that are taken as subjective culture. Atheists employed the ventral region of the mPFC during self-reflection, whereas believers of Christianity recruited the dorsal region of the mPFC, and Buddhists showed activations in the mid-cingulate cortex during self-reflection [33,34]. Moreover, the studies using a mediation analysis have demonstrated that the cultural group difference in brain activity engaged in different stimuli/tasks (e.g., TPJ activity during self-reflection [36] or neural activity in response to error responses [72]) can be partially or fully explained by a specific cultural value (e.g., interdependence).

Cultural priming studies that examined how brain activity varies as a consequence of recent access to specific cultural values or knowledge suggest direct interactions between culture and the brain. One line of research primed interdependent/independent self-construals by asking participants to read essays containing plural or singular pronouns ('we' or 'I') or to think how the self is similar to or different from others. It has been shown that priming independent versus interdependent self-construal in East Asians enhanced neural activity in the right frontal activity in response to one's own face [45], and in the mPFC and posterior cingulate cortex during self-reflection [47], and increased the neural activity to affective incongruity in the emotional expression of a central figure relative to the surrounding figures [73], as well as decreasing reward-related activity in the bilateral ventral striatum in response to winning money for a friend during a gambling game [74]. Priming interdependence versus independence decreased early sensory responses to painful electric shocks [43], increased motor-evoked potentials induced by transcranial magnetic stimulation during an action observation task [49], and increased local synchronization of spontaneous activity in the dorsal region of the mPFC – but decreased local synchronization of spontaneous activity in the posterior cingulate cortex during a resting state [50].

These findings indicate that both long-term and short-term cultural experiences influence the brain activity involved in multiple mental processes, and provide evidence for interactions between specific cultural traits and neurocognitive processes. In daily life, people can be imbued with different beliefs and learn new behavioral scripts by observing the behavior of others. These effects are important for children during education that plays a key role in modifying the functional organization of the brain. Brain activity changed even for adults who emigrated to a different culture such that they were able to understand others' mental states easily [70,71]. The direct interaction between culture and brain allows the development of culturally-specific patterned neural processes and provides a neural basis for behavioral acculturation.

Brain Guides Behavior to Fit into Cultural Environments

The culturally shaped brain guides behaviors that conform to specific social rules and fit into specific sociocultural contexts. For example, the enhanced activity in the TPJ in response to self-reflection [36], and in the caudate nucleus and mPFC in response to social subordination cues [37], in individuals in a collectivistic culture may provide a neural basis for these people to quickly take others' perspectives, coordinate with others, and behave according to social norms that emphasize social relationships. By contrast, the increased activity in the mPFC in response to self-reflection [36], and in the caudate nucleus and mPFC in response to social dominance cues [37], in an individualistic culture may motivate individuals to behave to reach their own goals and to behave according to social norms that emphasize social hierarchy. It is likely that the culturally patterned brain activity allows individuals to voluntarily take appropriate actions that easily fit into their own sociocultural environments (e.g., CV-behavior). A brain that lacks such culturally-specific functional organization, such as newly arrived immigrants, may have to engage more effort to conform to the behavioral scripts and social rules in a new cultural environment (e.g., CC-behavior).

Behavior Modifies Culture

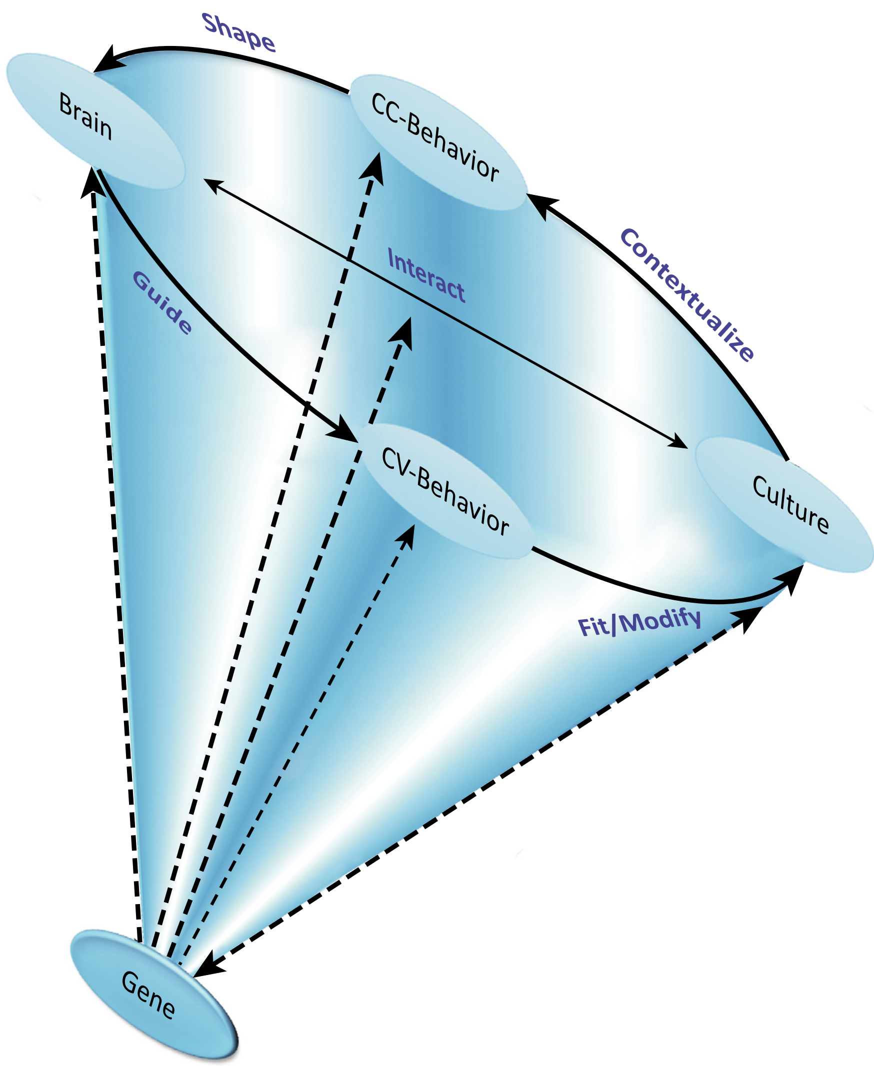
Human beings never stop modifying existing cultures. People derive cultural meaning from creative acts of innovative realization, and bring conventions from one society to another [75]. For example, novel ideas/concepts and behavioral scripts were created during the transition from a collecting/hunting society to a farming society and then to an industrial society [59]. Social behaviors produce new techniques that in turn generate new behavioral scripts and beliefs/values/norms. Social learning is another important behavior that helps to spread cultural beliefs among different social populations and over generations [76]. A recent example is the widespread use of the internet – that brings revolutionary changes of social communications and has created 'an internet culture' that is characterized by virtual acquaintance and frequent anonymous encounters with familiar or unfamiliar individuals [77]. The invention of the smartphone and other portable connected devices has liberated people from nine-to-five working at office but has created an 'always on' culture that blurs the boundary between work and life [78]. These behaviors bring forth new social values that can modify traditional cultures and are delivered from one generation to the next.

Genes and the CBB Loop

Given the long history of viewing human development as a joint outcome of genetic and environmental factors, it is crucial to clarify the relationship between genes and the CBB loop. At a societal level, relative to the timescale over which genes moderate the brain (e.g., thousands of years),

Key Figure

Illustration of the Relationship Between Genes and the CBB loop



Trends in Cognitive Sciences

Figure 2. Genes provide a fundamental basis for the CBB loop in several ways, including genetic influences on the brain and behavior, mutual interactions between genes and culture, and genetic moderations of the association between brain and culture. The unbroken lines in the CBB loop indicate fast interactions between two nodes, whereas the broken lines linking genes and the CBB loop indicate slow interactions between genes and the CBB loop. Abbreviations: CBB, culture–behavior–brain; CC-Behavior, culturally contextualized behavior; CV-Behavior, culturally voluntary behavior.

cultural and behavioral influences on the brain occur much faster (e.g., lifespan) [62]. Cultural priming on the timescale of minutes in a laboratory setting can even induce functional changes of brain activity during a variety of tasks [43–50]. Given that the brain changes associated with genetic and cultural factors operate at different speeds, we suggest that genes interact with the CBB loop by providing a fundamental basis for the CBB loop in several ways, as illustrated in Figure 2

Box 2. Gene × Culture Interaction and Brain Function

Behavioral research of gene × culture interaction compares genotyped individuals from different cultural groups and has shown that genetic effects on behavioral tendencies or psychological traits can be different or even opposite in East Asians (e.g., Koreans) and Westerners (e.g., North Americans) [90]. To date, there has been no parallel brain imaging research that examines gene × culture interaction on brain activity by comparing genotyped individuals from different cultural groups. However, recent fMRI studies that investigated associations between a cultural trait and brain activity in genotyped individuals from the same cultural group provided initial evidence for gene × culture interaction on brain activity. These studies examined the association between cultural values (i.e., interdependence) and brain activity involved in self-reflection in short/short (s/s) and long/long (l/l) allele carriers of the serotonin transporter promoter polymorphism (*5-HTTLPR/SCL6A4*) [92] and involved in empathy for pain in G/G and A/A allele carriers of oxytocin receptor gene (*OXTR* rs53576) [93] in a Chinese population. One study found that l/l (the minor allele in Chinese sample) but not s/s carriers of *5-HTTLPR* showed significant association between interdependence and activity in the medial prefrontal cortex, bilateral middle frontal cortex, temporoparietal junction, and insula during reflection on one's own mental attributes. The other study found that, relative to A/A carriers of *OXTR* rs53576, G/G carriers (again the minor allele in Chinese sample) showed stronger associations between interdependence and empathic neural responses in the insula, amygdala, and superior temporal gyrus. Although both studies tested individuals from one cultural group (i.e., Chinese), the findings of the two studies were similar in that one versus another single-nucleotide polymorphic variant showed a stronger link between a cultural value and brain activity. These findings suggest that a specific genetic polymorphism may interact with a cultural trait to shape neural activities underlying social cognitive and affective processes, and thus provide initial cultural neuroscience evidence for gene × culture interaction on brain function.

(Key Figure). First, genes shape human brain anatomy by influencing its size [79,80], affecting both cortical and subcortical structures [81,82], and shaping the functions of specific brain regions [83,84]. Second, twin and adoption studies have demonstrated that some behavioral/cognitive characteristics are heritable [85]. Candidate-gene and genome-wide association studies have linked genes to behaviors that are thought to be culturally determined (e.g., smoking and schooling) [86,87]. Third, our environment and experience strongly constrain how genotypes give rise to behavioral phenotypes [88]. Moreover, the link between genes and behavior is expressed in different or even opposite patterns in East Asian and Western cultures [89,90], and cultural difference in social orientations (e.g., interdependence) exist in one variant but not another variant of the same gene [91]. These findings indicate gene × culture interactions on behavior and psychological traits. Finally, the brain activity in responses to self-reflection and others' emotions varies as a function of cultural values (e.g., interdependence) among carriers of one variant of a gene but not of a different variant of the same gene [92,93] (Box 2). These cultural neuroscience findings implicate that genes may moderate the association between culture and brain. The model shown in Figure 2 is different from the macroscopic model of human development [51] that includes gene and culture in the same loop to influence the brain and behavior. Rather, the model in Figure 2 considers the different timescales along which gene and culture interact with the brain. This model not only emphasizes the interaction between genes and each node of the CBB loop but also highlights genetic contributions to the dynamic interaction between culture, behavior, and the brain, such as affecting how fast the interaction in the CBB loop occurs.

The findings of associations between collectivistic cultural values and allele frequencies of genes across nations [94,95] implicate potential mutual influences between genes and culture. On a lifespan scale, genes may affect the degree to which an individual is influenced by cultural contexts, given that some allele carriers are more susceptible to environmental influences than are carriers of other alleles [96,97]. Moreover, cultural experience may induce possible epigenetic changes that can be delivered across generations. On a historical timescale, culture may impact on both the social and physical environments within which genetic selection operates and shapes the human genome [54,98].

Predicting Brain Changes Based on the CBB Loop

The CBB loop model allows us to speculate on future dynamic brain changes by considering current culturally patterned behavior and relevant brain function. In addition, the CBB loop model predicts that related brain changes facilitate human adaptation to sociocultural environments. To take a recent example, the rapid growth of internet commerce and communication has created 'an internet culture' [77] that has changed human behaviors substantially and may lead to modifications of brain function. For instance, the internet search engines allow students to access a large body of literatures from internet databases. They now have to learn where and how to access these literatures rather than to remember their contents [99]. Thus, the neural structures that are currently used to store and retrieve semantic knowledge (e.g., the inferior frontal cortex, inferior parietal lobe, and temporal lobe) [100,101] may be endowed with other functions such as inference of causal relationships [25] in the next generation. Another consequence of the emerging internet culture is the abatement of close-distance face-to-face communications that allow humans to develop unique neural activity supporting reactivity to the cognitive and affective mental states of others [102]. Children who increasingly rely on internet/smartphone communication may spend less time engaging in close-distance face-to-face interactions, which may in turn influence brain activity in the mPFC, TPJ, and anterior cingulate – areas related to the inference of others' mental states and empathy [38–41]. Internet and smartphone also keep people continuously digitally connected and this 'always-on' culture [78,103] leads to a high level of discontinuity in the execution of activities [104] related to multiple tasks that may bring various changes of the brain functions of the frontal and parietal lobes related to attention [105]. These potential changes of brain functions, which should be tested in future empirical research, may help the next generation to easily fit into the internet culture and, meanwhile, the brain shaped by the internet culture may produce new behavioral scripts (e.g., online shopping and social networking) that may modify the contemporary sociocultural environment.

Concluding Remarks

Although cultural neuroscience findings related to the CBB loop model of human development are mainly derived from studies of individuals from East Asian/Western cultures, this model can advance our understanding of the relationships between culture, behavior, and the brain in general. The CBB loop model gives prominence to the dynamic features of CBB interactions that allow continuous changes of culture, behavior, and the brain. The CBB loop model proposes cultural and genetic modifications of the functional organization of the brain along different timescales, and this has important implications for understanding the role of the brain in bridging the gap between gene and culture during gene-culture coevolution and gene × culture interactions. The dynamic properties of the CBB loop also have implications for comprehending human success during evolution. The CBB loop model helps us to predict future changes of human brain function as a result of emergence of new culture, and raises new questions for future research (see Outstanding Questions).

Outstanding Questions

Whether and how do cultural experiences lead to epigenetic changes of brain activity underlying cognition and behavior?

Whether and how do cultural experiences affect human brain at the molecular (e.g., neurotransmitter) level, given the increasing neuroimaging evidence for cultural influences on brain activity in different regions?

Can a cultural neuroscience approach reveal the cultural traits that interact most strongly with genetic makeup to shape the functional organization of the human brain?

What is the genetic basis of fast interactions in the CBB loop? How can we address this issue by comparing behavior and brain activity in humans and other primates?

Who, the majority or minority in terms of allele frequency in a genetic population, contribute more to create novel culture and can most easily fit into new sociocultural contexts?

How do new beliefs and behavioral scripts emerge during the interaction between culture, behavior, and the brain? What are the adaptive effects of technological culture on human mind and behavior?

Whether and how do globalization and cultural exchanges affect the observed cultural group differences in brain activity? Will cultural differences in brain activity observed in current societies decrease or increase in future?

Acknowledgments

This work was funded by the National Natural Science Foundation of China (Projects 31421003, 31470986, 91332125), the Ministry of Education of China (Project 20130001110049), and the Leverhulme Trust, United Kingdom. We thank Michele Gelfand, Glyn Humphreys, Georg Northoff, Peter Richerson, and Andreas Roepstorff for their helpful comments on the manuscript.

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