67 The Cultural Neuroscience of Human Perception

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ABSTRACT Culture and the brain were once thought of as mutually exclusive views on behavioral variation—an idea that is changing with the emerging field of cultural neuroscience. In this chapter, we discuss recent research examining the interplay of cultural and genetic factors on the neural bases of human perception. We conclude that cultural experience readily impacts basic mechanisms underlying perception, ranging from lower-level nonsocial domains (e.g., attentional deployment and object perception) to higher-order social domains (e.g., emotion recognition and theory of mind). More broadly, we discuss the promise and pitfalls of a cultural neuroscience approach to psychological processes and explain how this multilevel approach can contribute to both cognitive neuroscience as well as to social and cultural psychology.

The cultural neuroscience of human perception

Humans are biological systems embedded in larger social systems. We see, think, and act in the context of others. We exist in cultural environments in which specific meanings, practices, and institutions organize our perceptual, cognitive, and behavioral tendencies. In spite of this fact, culture and the brain were once thought of as mutually exclusive views on variation in behavior and were subjects of study divided by relatively strict divisions across the natural and social sciences. Although it is clear now that culture and social experience may readily shape brain function, this was not always the case. Even with respect to more general, nonsocial experience, the broader field of cognitive neuroscience early on was surprised by such influences on the brain. In the early 1990s, Posner (1993, p. 674) remarked in Science: "If the neural systems used for a given task can change with 15 minutes of practice ... how can we any longer separate organic structures from their experience in the organism's history?"

The answer, we now know, is simply that we cannot. Recent research examining the neural mechanisms underlying the effects of cultural experience on the brain and, conversely, examining how the brain gives rise to cultural experience has led to the emergence of a new field: cultural neuroscience (Ambady & Bharucha, 2009; Chiao & Ambady, 2007; Han & Northoff, 2008; Han et al., 2013; Kitayama & Park, 2010). Accumulating evidence for neuroplasticity and the coextension of culture and the brain has made clear that cultural and neural processes are not inherently distinct objects of inquiry; instead, they may richly interact. A complete and accurate understanding of behavioral variation requires the comprehensive study of these tandem processes.

Arguably, the human brain evolved to permit elaborate social behavior, particularly so that such behavior may be adapted to the social structures and patterns in which individuals find themselves. Cultural neuroscience is centered around the assumption of a bidirectional relationship between culture and the brain: the brain adapts to cultural processes, and cultural processes adapt to neural constraints (Ambady & Bharucha, 2009). As such, this burgeoning field aims to provide a fuller understanding of psychological phenomena at multiple levels of analysis.

Neuroplasticity

Progress in the emerging field of cultural neuroscience has been bolstered by accumulating evidence for neuroplasticity. The human brain has long been known to be intrinsically malleable, with environmental and experiential factors determining both its function and structure. Occipital regions centrally involved in vision, for example, can be recruited to process sounds in blind individuals (Gougoux et al., 2009), and primary auditory cortex can be co-opted to process visual stimuli in deaf individuals (Finney et al., 2001). Thus, in the face of impairments, the brain is able to flexibly reorganize itself. Even beyond recovering from impairments, recent evidence has documented the astounding flexibility of neural mechanisms to high-level social and cultural experience.

Consider a study examining the influences of juggling experience on neural activity. All participants lacked juggling experience; half were asked to teach themselves to be able to juggle for at least one minute continuously, and were given three months to practice. Following the three months, voxel-based morphometry revealed that those who had learned to juggle exhibited increased gray matter in two areas associated with visual and motor activity-the mid-temporal area and the posterior intraparietal sulcus. After an additional three months, during which the participants had stopped juggling, these regions' gray matter returned to original size (Draganski et al., 2004). In another study, expert male dancers underwent functional MRI (fMRI) while watching videos of various dance moves. When viewing dance moves that the experts had been trained to perform relative to moves they had not, the experts showed greater activation in regions associated with the mirror neuron system involved in the action simulation, including the premotor cortex, posterior intraparietal sulcus, and posterior superior temporal sulcus (STS; Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005).

Similar effects for experience and exposure on neural activation were found in a study on taxi drivers in London (Maguire et al., 2000). London taxi drivers undergo extensive training over a two- to four-year period that involves learning, among other things, the layout of 25,000 streets in the city in order to obtain an operating license. Using voxel-based morphometry, Maguire and colleagues found that the gray matter volume of the posterior hippocampus was enlarged and anterior hippocampus gray matter volume was reduced in London taxi cab drivers, when compared with an age-matched control group. Further, hippocampal volume was positively correlated with taxi-driving experience. The longer the taxi drivers had driven in London, the greater the posterior hippocampal gray matter volume and the more decreased the anterior gray matter volume. This suggested that environmental demands and, specifically, spatial navigation experience due to one's chosen occupation, dynamically shapes the structure of the hippocampus. Together, all these studies show that the brain continually adapts to the cultural environment and is plastic with respect to both its function and structure. Such work has been critical in providing a foundation for a neuroscience of culture.

Culture mapping and source analysis

There are two overarching goals of the emerging field of cultural neuroscience (Ambady & Bharucha, 2009). The first goal is for researchers to map out the differences and similarities across cultures at the behavioral and neural levels—that is, the goal of *cultural mapping*. The majority of past research in cultural neuroscience fits within the purview of this goal, seeking to understand the tuning of neural processes to the cultural environment. On the one hand, cultural mapping can show how the environments or cues of different cultures are processed differently by individuals from a given culture. Alternatively, culture mapping can show how the same environment or same cues are processed differently by individuals from different cultures. Culture mapping can also reveal how identical cues are processed differently across cultures.

Once such multilevel cultural convergences and divergences are mapped out, the second, perhaps more challenging, goal of cultural neuroscience is to determine the actual sources or causes of these differences and similarities—that is, the goal of *source analysis*. By and large, cultural neuroscience studies typically compare two different cultural groups (e.g., Americans and Chinese), with the assumption that behavioral and neural differences that arise are due to the wealth of cultural learning, experiences, and contexts that pervade the lives of those two groups. However, in some cases that assumption may be premature, as the cultural factors may covary with genetic factors.

Although the vast majority of genetic variation exists within populations (~93–95% of genetic variation; Rosenberg et al., 2002), there is variation between populations of different ancestral origins (~3–5% of genetic variation). Thus, it is possible that cognitive and neural processes associated with specific genes that vary in allelic frequency may show variable functioning across populations, independent of cultural influences. Indeed, more than 70% of genes are expressed at the neural level (Hariri, Drabant, & Weinberger, 2006). Thus, one major question in cultural neuroscience is the extent to which behavioral and neural differences across cultures arise due to cultural versus genetic factors, or their unique interaction (Chiao & Ambady, 2007; Way & Lieberman, 2010).

There a number of genes important to brain and behavior that show variation in allelic frequency across geographical regions, including the serotonin transporter (5-HTTLPR) and dopamine D4 receptor (DRD4) exon III polymorphisms. For example, evidence indicates that the S allele of 5-HTTLPR is associated with increased negative emotion and heightened anxiety, and the S allele is more prevalent in East Asian populations (e.g., 70-80% S carriers) relative to other nations (e.g., 50% or less S carriers). Recently, Chiao and Blizinsky (2010) examined the prevalence of 5-HTTLPR in different countries and correlated the relative proportion of short and long alleles in each population with a measure of individualism and collectivism for each country. Overall, Western societies tend to be characterized by independence and individualism, emphasizing individuals' goals and achievements. East Asian societies, on the other hand, tend to be more interdependent and collectivist, emphasizing relationships, and roles. Chiao and Blizinsky found that 5-HTTLPR S carriers were considerably more prevalent in collectivistic relative to individualistic populations. Counterintuitively, however, collectivist populations contain considerably fewer depressed individuals, while having an increased frequency of the 5-HTTLPR short allele linked to heightened anxiety and depression. Chiao and Blizinsky argued that this seeming paradox may be explained by cultural ideology and norms of collectivism that act as a buffer and provide social support in those populations. This interpretation is tentative but suggests that the unique interplay of cultural and genetic factors may have a profound impact on brain and behavior.

Human perception

Cultural psychologists have long documented that culture can exert a deep influence on the way individuals think and behave. Culture influences how we perceive ourselves and others (Markus & Kitayama, 1991) as well as how we perceive and interpret more basic, lower-level visual and perceptual cues. Some of the biggest strides in cultural neuroscience have come from the domain of human visual perception.

Two cultures whose social structure and practices differ considerably in such a way as to influence visual processing are Western culture and East Asian culture. As mentioned, Western societies tend to be more individualist and independent, whereas East Asian societies tend to be more collectivist and interdependent. These two different sociocultural systems are known to give rise to dissimilar patterns of cognition (Nisbett, Peng, Choi, & Norenzayan, 2001). Recent work has shown that these systems are also likely to influence visual attention to aspects of the environment (e.g., Kitayama, Duffy, Kawamura, & Larsen, 2003; Masuda & Nisbett, 2001). Specifically, practices and ideas in Western societies tend to require separating objects from their contexts and interpreting independent and absolute aspects of environmental stimuli (i.e., analytic thinking). Practices and ideas in East Asian societies, however, tend to require interpreting objects in conjunction with their context and understanding the relatedness among environmental stimuli (i.e., holistic thinking). In contrast, Western societies (emphasizing independence) place more value on salient objects and one's own relationship to those objects. This should lead to Westerners directing more attention to these, without as much concern for context. Indeed, East Asians are more likely

to perceive objects and scenes as wholes and to pay attention to contextual information (referred to as holistic perception), whereas Westerners are more likely to perceive objects and scenes according to their distinct parts and ignore contextual information (referred to as analytic perception; Nisbett et al., 2001; Nisbett & Miyamoto, 2005).

OBJECT PERCEPTION Overall, Americans engage in more analytic perception and Japanese engage in more holistic perception. The framed-line test (Kitayama et al., 2003) has been especially useful in demonstrating how these two cultures shape divergent patterns of visual perception and attentional deployment. In the framed-line test, participants are shown a square figure with a vertical line hanging from its top edge (but not spanning the entire height of the square), located in the horizontal center. After briefly inspecting this arrangement, participants are shown a new square figure of a different size. In the absolute condition, participants are asked to draw a line in this new square that is identical in absolute length to the vertical line previously seen. In the relative condition, however, they are asked to draw a line that has identical proportion to the context (i.e., the surrounding square frame) as that of the vertical line previously seen. Thus, performance in the absolute task depends on analytic processing of a salient stimulus and characteristics that are independent of context. Performance in the relative task, however, depends on holistic processing that includes the surrounding square frame, and the relationship between the salient stimulus and its context. Consistently, Americans perform better in the absolute task than in the relative task, whereas Japanese show the reverse pattern, performing better in the relative task than in the absolute task (Kitayama et al., 2003).

Building on these behavioral findings, Hedden and colleagues (2008) examined neural activity during this task using fMRI. Participants were asked to judge the size of a vertical line either incorporating (relative condition) or ignoring (absolute) contextual information, the surrounding square frame. Results revealed cultural variation in neural responses to the extent that distinct brain regions were recruited to perform the relative and absolute line judgment tasks in relation to the perceiver's culture. Participants recruited frontal and parietal regions associated with attentional control to a greater extent when engaged in a task that was incongruent with their cultural patterns. Thus, activity in frontoparietal regions increased when people of East Asian descent ignored contextual information and people of European descent incorporated contextual information during line size judgments. Moreover, the degree of activation during the incongruent relative to the congruent judgment task was negatively correlated with degree of individualism in people of European descent and the degree of acculturation in people of East Asian descent. Thus, the brain's attentional network was more strongly engaged by culturally nonpreferred perceptual judgments. This line of work also illustrates how cultural experience modulates the function of neural mechanisms in a sensitive, graded fashion.

Beyond somewhat simplistic line and frame stimuli, Gutchess, Welsh, Boduroglu, and Park (2006) converged on similar results in higher-level object perception. East Asian Americans and non-Asian Americans performed a task involving the recognition of complex pictures showing an object against a background while their neural responses were measured using fMRI. East Asian Americans and non-Asian Americans performed equally well but recruited distinct brain regions during the task. Non-Asian Americans showed more activation in the object-processing areas in the ventral visual cortex than did the East Asians, who showed more activation in the left occipital and fusiform areas associated with perceptual analysis. Goh and colleagues (2007) also found that elderly East Asian, Singaporean participants showed less of an fMRI adaptation response in object-processing areas compared to older Western adults. Westerners who were presented with images of an object showed reduced neural activation to the object with subsequent presentations, indicating that they had adapted to seeing the object. In contrast, East Asians continued to show an equally strong neural response during subsequent presentations of the same object, with all iterations showing a response as if they were seeing the object for the first time. These findings suggest that Westerners allocate greater attention to objects than do East Asians, whose attention may be directed elsewhere (such as to the background).

Thus, a perceiver's cultural background shapes the neural mechanisms underlying the perception of objects and their surrounding context in a manner adaptive for the values of one's culture. Culture equips individuals with different perceptual strategies that are evident at the behavioral and neural levels.

EMOTION PERCEPTION Successfully reading others' emotions is important because they avail the perceiver with information about upcoming behaviors or environmental conditions. As others' facial expressions warn and ready perceivers for impending action, and because such actions are most likely to happen within one's culture, the emotions that are most ecologically relevant are those that are expressed by members of one's own culture (Weisbuch & Ambady, 2008). Indeed, it has been proposed for over two decades that one's cultural background may influence the recognition of others' emotions (Lutz & White, 1986). Thus, one question of interest to cultural neuroscientists is whether members of a given culture exhibit a selective ability to recognize the emotions of members of one's own culture. It is possible that acculturation leads to the unique tuning of the perceptual system to emotional expressions of other members of that same culture. Elfenbein and Ambady (2002b) conducted a metaanalysis of studies involving face emotion-recognition tasks across multiple cultures. Indeed, analysis of the results from these studies led to the conclusion that individuals are better at recognizing own-culture expressions relative to other-culture expressions, pointing to a robust cultural specificity in emotion recognition.

An early cultural neuroscience study examined the neural basis of this cultural specificity. American and Japanese participants were presented with American and Japanese faces exhibiting angry, fearful, happy, or neutral expressions. Both American and Japanese participants showed a significantly greater bilateral amygdala response to the perception of fear faces when posed by same-culture, ingroup members as compared to fear expressions posed by other-culture, outgroup members. Thus, American participants showed a stronger amygdala response to fearful American faces, and Japanese participants showed a stronger amygdala response to fearful Japanese faces. No significant differences were observed for anger, happy, or neutral expressions (Chiao et al., 2008). One possible explanation for these results is that a fear expression may have particular communicative value for ingroup members because it provides information about dangers in the environment that might be especially relevant to them. In addition, expressions of fear may be particularly valuable for eliciting the help of others (Marsh, Kozak, & Ambady, 2007). Recognizing fear signals from ingroup members might motivate helping behavior and contribute to the success and survival of the group. Thus, the amygdala exhibits selective responses to own-culture fear displays, providing a neural correlate of the cultural specificity in emotion recognition.

A more recent study found that culture influences neural responses to fear faces depending on the direction of gaze. In Western cultures, eye gaze is generally seen as a sign of respect (Argyle, 1976). A failure to make eye contact may therefore be seen as disingenuous. In East Asian cultures, however, direct eye contact can be perceived as impolite and inappropriate. In these cultures, averted eye gaze, especially downward shifts in gaze, is generally perceived as respectful (Knapp & Hall, 2002). Eye gaze also affects the perception of emotions. For instance, Adams and Kleck (2003, 2005) found that direct relative to averted gaze affected perceptions of approach-oriented emotional facial expressions (e.g., anger and joy) by facilitating speed of processing and increasing recognition accuracy. Averted relative to direct gaze, on the other hand, exerted a similar influence on the perception of avoidanceoriented emotions (e.g., fear and sadness). Within the same culture, a differential neural response in the amygdala has also been found to direct-gaze as compared to averted-gaze emotional faces (Adams, Gordon, Baird, Ambady, & Kleck, 2003).

In one recent fMRI study, both Japanese and US participants showed stronger neural activation to sameculture fear faces with averted gaze and other-culture fear faces with direct gaze in several areas of the brain associated with face, gaze, and emotion processing such as the bilateral fusiform gyri, the left caudate, and the right insula (Adams, Franklin, et al., 2010). Interestingly, however, all participants showed greater activation in face-processing areas, such as the bilateral fusiform gyri, to direct relative to averted gaze when displayed on Japanese faces, whereas the opposite was true for US Caucasian faces. This finding suggests that both Japanese and US Caucasian participants may share a common understanding of the distinct cultural meanings associated with gaze behavior. In this case, participants from both cultural groups showed greater activation to incongruous eye gaze behaviors, based on what is generally considered most culturally appropriate. This finding indicates that social expectations and cultural norms may be transmitted and processed consistently across different cultures. Further, underlying an overall behavioral difference across two cultures, one set of neural mechanisms may exhibit an analogous difference in responding, whereas other mechanisms may exhibit a cultural convergence.

Such simultaneous convergence and divergence was also observed in a study by Freeman, Rule, Adams, and Ambady (2009). American and Japanese participants were presented with figural outlines of dominant and subordinate bodily displays (figure 67.1A). In response to the same bodily cues, reward-related mesolimbic regions including the head of the caudate nucleus, bilaterally, and a dorsal aspect of the medial prefrontal cortex showed a mirror-image pattern of responding across the two cultures. Specifically, the caudate and medial prefrontal cortex showed stronger responses to dominant displays in Americans, whereas these same regions showed stronger responses to subordinate displays in Japanese individuals (figure 67.1B). Further, the magnitude of activation in these regions was related to self-reported dominant or subordinate behavioral tendencies. These mesolimbic regions are typically activated by rewarding and motivationally significant stimuli, and in responding to such stimuli they help to coordinate learning and behavior. This finding suggests that perceiving other individuals' nonverbal power displays triggers reward-related responses that may help contribute to high-level social behaviors. Moreover, the results demonstrate additional neural correlates of the individualism characteristic of Americans, emphasizing dominance and elevation of the self, versus the collectivism characteristic of Japanese individuals, emphasizing deference and obligation to others, elevation of one's social group, and subordination.

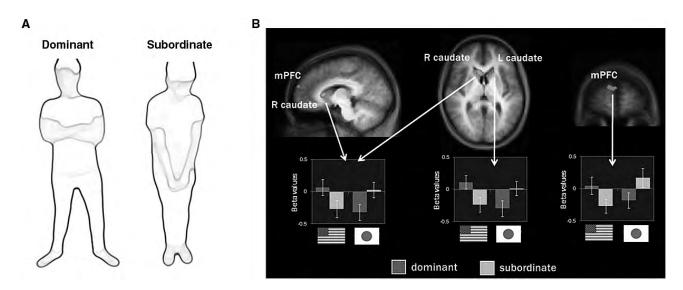


FIGURE 67.1 Cultural specificity to (A) dominant and subordinate figural outlines in (B) caudate and dorsal medial prefrontal cortex (mPFC) response. (Adapted from Freeman et al., 2009.) (See color plate 56.)

MIND PERCEPTION Beyond recognizing expressions of the face or body, the ability to understand others' thoughts is one of the most defining attributes of human behavior (e.g., Saxe & Baron-Cohen, 2006). It is often referred to as "theory of mind," since it requires theorizing that others have minds like one's own and that one may therefore be able to use one's own mind to understand what is occurring in others' minds (see Gallagher & Frith, 2003, for a review). Naturally, the ability to infer the internal states of others' minds is susceptible to broader cultural influences.

Kobayashi, Glover, and Temple (2007) examined theory of mind by using false-belief and cartoon tasks with 8- to 12-year-old American and Japanese children while measuring their brain responses using fMRI. In a typical false-belief task, someone places an object into a cupboard in the presence of an observer. The observer then leaves and the object is moved from the cupboard to another location. The test, then, is to see whether the child will understand that the observer still thinks the object is in the original location-the cupboard (since this is where the observer saw it placed) or if the child will mistakenly apply his or her own knowledge about the object's true, current location. A child with a theory of mind should be able to take the perspective of the observer and assume the observer will look for the object in the cupboard. The study found activation in the ventromedial prefrontal cortex and precuneus across both groups of children, suggesting these areas are important for universal understanding of intentionality. But there was also evidence of cultural specificity in other brain areas. Japanese children showed stronger activation in the inferior frontal gyrus, similar to Japanese adults in a previous study by the same group. Thus, the neural substrates underlying the understanding of others' intentions do seem to be affected by culture. A more recent study was able to clarify these findings.

Behavioral data suggests that people are better at reading the minds of others from their own cultures as compared to those from other cultures (Adams, Rule, et al., 2010). The "reading the mind in the eyes" test involves presenting participants with cropped photographs of faces so that only the eyes are visible and was developed by Baron-Cohen and his colleagues (Baron-Cohen, Wheelwright, Hill, Raste, & Plump 2001). Participants have to choose from adjectives that best describe the target's mental state. This task is believed to require the perceiver to take the perspective of the target in order to infer his or her state of mind. Individuals who lack mental inference abilities (such as patients with neurological damage) show severe impairment in choosing which adjectives best describe the targets' mental states (Adolphs, Baron-Cohen, &

Tranel, 2002). Adams et al. (2010) found that ownculture "reading the mind in the eyes" judgments more strongly engaged the STS, a region important to social inferences and theory of mind. Specifically, American participants showed stronger bilateral STS activity when inferring the mental states of American targets, and Japanese participants showed stronger bilateral STS activity when inferring the mental states of Japanese targets (figure 67.2). Thus, culture equips its perceivers with a culturally tuned ability to infer others' mental states, reflected in activity of the STS. In this case, the eyes of different cultures are differentially processing in the STS, with preference for one's own culture.

Conclusion

The emergence of cultural neuroscience thus far has allowed for a deeper understanding of the processes underlying human perception. This new field has shed light on the nature of cross-cultural similarities and differences previously observed in behavioral work, and extended our understanding of the phenomena to the neural level. We reviewed evidence showing that culture shapes basic perceptual processes at varying levels of complexity and across both nonsocial and social domains. We highlighted how aspects of the sociocultural environment shape perceptual processing and give rise to culturally specific behavioral and neural responses. Much of this research involved identifying the neural correlates of established cross-cultural differences in perception. As discussed earlier, however, there is an increasing focus on the interplay of genetic and cultural factors; we expect this can only continue, as the role of culture-gene interactions becomes easier to examine with methodological advances and increases in the ability to measure genetic polymorphisms.

In addition, a cultural neuroscience approach to human perception holds great potential for an increased understanding of how culture influences behavior, the mind, and the brain more broadly. For instance, one way to examine plasticity is to examine how the brain changes with exposure to a new culture. Examining the unique effects of acculturation in immigrants and how cultural influences manifest at the neural level in bicultural and multicultural individuals will be of great importance. Interestingly, there might be critical stages-stages of development during which the brain is more likely to change than other stages-that future research could address (Han et al., 2013). Cultural neuroscience shows promise in helping not only to understand the neural basis of psychological processes, but also in helping to uncover the plasticity of the brain's response to its culture and environment.

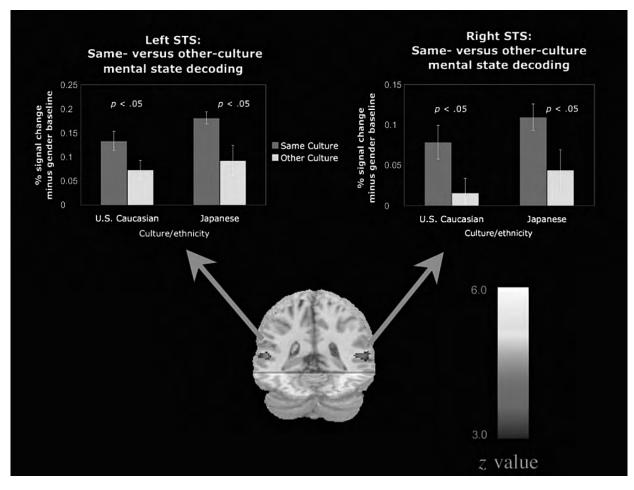


FIGURE 67.2 Cultural specificity in (A) left and (B) right posterior superior temporal sulcus (STS) response to the

That being said, there are a number of logistical challenges in conducting research in the area of cultural neuroscience. Attention must be paid to ensure proper control is implemented, given differing scanner sites. Further, almost all the recent discoveries in cognitive neuroscience have come from richer industrialized nations. For example, to our knowledge, there have been no studies in cultural neuroscience in Africa, South America, or the Middle East. Within the field of psychology, 95% of psychological samples come from countries with only 12% of the world's population (Arnett, 2008), typically Western industrialized nations (Henrich et al., 2010). Within the field of human neuroimaging alone, 90% of peer-reviewed neuroimaging studies come from Western countries (Chiao & Ambady, 2007). Nevertheless, the cultural neuroscience framework represents an unprecedented opportunity to link human diversity across multiple levels of analysis, from genes and brain to mind and behavior. As outlined throughout this chapter, it is revealing novel insights into the influences of culture

reading the mind in the eyes (RME) task. (Adapted from Adams et al., 2009.) (See color plate 57.)

on a broad range of perceptual phenomena at multiple levels of analysis, from lower-level attention to higher-order social processes. Advances in concepts and methodology in cognitive neuroscience provide a solid foundation for examining the mutual interplay of cultural, neural, and genetic forces throughout the life span.

Historically, psychology has vacillated in its focus; at some times, popular approaches focus on influences of learning, experience, and culture, and at other times they focus on innateness and fixity. Like most dichotomies, rarely does either side provide a full and complete characterization of the phenomenon. Theoretical and empirical work identifying the various factors underlying what is learned and what is innate and how they interact will be critical, and the cultural neuroscience approach would seem highly promising in this regard. The cultural neuroscience approach provides the exciting opportunity to examine the mutual interplay of culture and biology across multiple levels of analysis, from genes and brain to mind and behavior, and ultimately to move toward a more complete and accurate understanding of human perception.

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