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Culture and neuroscience: additive or synergistic?

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The investigation of cultural phenomena using neuroscientific methods—cultural neuroscience (CN)—is receiving increasing attention. Yet it is unclear whether the integration of cultural study and neuroscience is merely additive, providing additional evidence of neural plasticity in the human brain, or truly synergistic, yielding discoveries that neither discipline could have achieved alone. We discuss how the parent fields to CN: cross-cultural psychology, psychological anthropology and cognitive neuroscience inform the investigation of the role of cultural experience in shaping the brain. Drawing on well-established methodologies from cross-cultural psychology and cognitive neuroscience, we outline a set of guidelines for CN, evaluate 17 CN studies in terms of these guidelines, and provide a summary table of our results. We conclude that the combination of culture and neuroscience is both additive and synergistic; while some CN methodologies and findings will represent the direct union of information from parent fields, CN studies employing the methodological rigor required by this logistically challenging new field have the potential to transform existing methodologies and produce unique findings.

Keywords: cross-cultural; cross disciplinary; cultural-neuroscience; culture; neuroscience; neuroimaging

INTRODUCTION

Cultural neuroscience (CN) is an emerging field focused on the bidirectional interaction between cultural experience and the brain (Chiao and Harada, 2008). Cross-cultural psychology has identified cultural variation in many domains of behavior (Jahoda and Krewer, 1997); at the same time, the neurosciences have identified mechanisms of neural plasticity from the molecular to the systems level (Berlucchi and Buchtel, 2009). Thus, investigating the neural underpinnings of cross-cultural behavioral variation seems like a logical next step. Yet, because this cross-disciplinary endeavor represents the integration of a social science, cross-cultural psychology, and a biological science, neuroscience, the concept of CN has been met with skepticism (Chiao and Ambady, 2007). How can something as complex and abstract as 'culture' be studied with methodologies that are concrete and quantitative? Furthermore, will CN be greater than the sum of these parent disciplines by yielding truly novel discoveries? Or will neuroscience merely identify brain regions associated with known cross-cultural differences while cross-cultural psychology provides comparable examples of behavioral variation to those already studied in neural plasticity research?

We argue that the combination of cross-cultural psychology and neuroscience is both additive—some CN methodologies and findings will represent the direct union of information from parent fields—*and* synergistic, having the potential to transform existing methodologies and yield truly novel findings. We use this additive/synergistic framework throughout our review to differentiate potential contributions of CN that represent extensions of work in parent fields from those that are truly novel.

Our review is organized into four sections. In the first section, we discuss the conceptual and methodological contributions of cross-cultural psychology and neuroscience to CN by describing relevant studies of cross-cultural behavioral differences and experience-dependent neural plasticity. We also outline methodologies from cross-cultural psychology and neuroscience that address challenges common to these fields and CN. Based on these translational methodologies, in the second section, we propose a set of methodological guidelines for CN studies. We intend these guidelines to aid CN researchers in fully capitalizing on the well-developed methodologies of these parent fields. In the third section, we evaluate current CN studies in terms of our guidelines in order to assess the current state of the field and suggest avenues for future growth. Finally, in the fourth section we summarize the contributions of parent fields to CN and discuss the additive and synergistic findings CN may yield.

HOW CROSS-CULTURAL PSYCHOLOGY AND NEURAL PLASTICITY RESEARCH CAN INFORM CULTURAL NEUROSCIENCE

Cross-cultural behavioral variation

Cross-cultural variation in human behavior has been described in all areas of human cognition (Jahoda and

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Krewer, 1997). In this section we describe cross-cultural psychology and psychological anthropology studies from domains of cognition currently being investigated in CN: language, perception and social cognition. The cross-cultural differences in behavior identified by such studies provide useful starting points for CN studies of the neural basis of cultural experience-dependant plasticity. Also, the theoretical and ethnographic background presented in these studies can generate testable hypotheses for CN to explore.

Language is one of the most prominent domains of cross-cultural research. Although there is not always a one-to-one relationship between language and culture, an individual's language(s) and cultural experience are inextricably linked (Nida, 2003). Language-specific syntax (Sera *et al.*, 2002; Bastiaanse and Edwards, 2004), phonology and orthography (Cheung *et al.*, 2001; McBride-Chang and Kail, 2002; McBride-Chang *et al.*, 2005) influence other aspects of language, such as language learning. For example, Cheung *et al.* (2001) found that both phonological complexity and orthography impact phonological awareness by comparing pre-reading and literate children who speak alphabetic and non-alphabetic languages of different levels of phonological complexity. CN studies have begun to identify the neural correlates of such cross-linguistic differences (Kochunov *et al.*, 2003; Valaki *et al.*, 2004; Bolger *et al.*, 2005). The extensive cross-linguistic literature will provide detailed background and testable hypotheses for future CN studies.

The relationship of language-specific structure and semantics to cognition is also studied in domains such as color and spatial perception (Byrnes and Gelman, 1991); however, whether language structures thought (cf. Whorf, 1956), or language and thought are largely independent (cf. Jackendoff, 1983) remains under debate. For example, despite wide variation in the number of color categories in different languages, color categorization has a predictable cross-linguistic structure related to the physiology of the human visual system (Abramov and Gordon, 1994; Kay and McDaniel, 1978), suggesting that color perception and categorization is physiologically rather than linguistically determined. In contrast, several studies have suggested that linguistic color categories influence color recognition memory and discrimination (e.g. Lantz and Stefflre, 1964; Roberson *et al.*, 2005), suggesting that language may influence higher-order aspects of color perception. CN research may shed light on the language and thought debate by providing information about the maliability of neural regions underlying different cognitive functions.

Perceptual domains unrelated to language, such as context sensitivity and visual illusion susceptibility, have also been found to vary cross-culturally (Segall *et al.*, 1963; Nisbett and Miyamoto, 2005). For example, Segall *et al.*, (1963) found substantial differences in the geometric optical illusion susceptibility of individuals from 17 different cultural groups. Three European groups were more susceptible to two of four illusions administered, while 14 non-European groups were more susceptible to the other two illusions. The authors deduced that cross-cultural variation in susceptibility to the illusions studied was likely related to perceptual habits acquired in different ecological and cultural environments. For example, rectangularity was widespread in the urban environments common among the European groups and much less widespread in the plains and equatorial forest dwellers in the non-European samples. Thus, the influence of cultural experience on behavior can be seen in cognitive domains as basic as visual perception suggesting that perceptual neural systems may also be fruitful areas of exploration for CN research.

One of the most productive areas of cross-cultural comparison is social cognition. Two theoretical frameworks that have dominated this field are are the classification of cultures as either individualistic or collectivistic (Triandis, 1995; Kagitçibasi, 1996) and the classification of individuals as having either an independent or interdependent self-construal (Markus and Kitayama, 1991; Killen and Wainryb, 2000). Here I will focus on the more prevalent framework, individualism/collectivism (IC), however these two frameworks are closely related and studies utilizing both frameworks have yielded similar results. Individualism is characterized by the assumption that individuals are separate in identity and responsibility from one another, and is typically associated with Western cultures. Collectivism is characterized by the idea that individuals are defined by and obligated to their social groups and is typically associated with East Asian cultures. The individualism/collectivism (IC) framework has been used to explain cross-cultural differences in visual perception, causal attribution, motivation and emotion (Kagitçibasi, 1996). Research on IC has been criticized because these concepts are applied broadly and are often not treated as independent constructs, but rather as two ends the same continuum (Schwartz, 1990; Fiske, 2002). In line with this assessment, Oyserman *et al.* (2002) performed a meta-analysis of IC studies and found that individualism and collectivism are indeed independent constructs, are not robust to measurement technique variation, and are not closely aligned with the East/West dichotomy, i.e. Westerners are not reliably more individualistic and less collectivistic than Easterners. Despite these criticisms, as of 1994, one-third of cross-cultural studies employed IC in their explanation of cross-cultural differences (Hui and Yee, 1994), and many CN studies described later in this manuscript also rely heavily on IC. Thus it seems the IC framework will continue to be prominent in cross-cultural studies; however, future CN investigations will be able to more effectively investigate the neural correlates of IC by paying careful attention to critical analyses of the IC framework in cultural anthropology and psychology.

Cross-cultural methods

Van de Vijver and Leung (1997) argue that 'culture is too global a concept to be used as a meaningful independent variable in the interpretation [of observed cultural differences]' (pp. 260). The challenge of establishing specific causation in cross-cultural comparisons is that cultures do not represent true experimental treatments—individuals cannot be randomly assigned to cultural groups, and culture entails a whole suite of correlated behavioral traits (Van de Vijver and Leung, 1997). Even cross-cultural elements that appear similar may result from different historical, environmental and psychological influences (Boas, 1896). The causes of between-group cultural differences are therefore difficult to identify. In cross-cultural psychology, a general strategy for establishing causation is to deconstruct culture into psychologically relevant components and use these components to design more tractable and controlled experiments (Van de Vijver and Leung, 1997). Cross-cultural psychology provides several methods to facilitate this deconstruction of culture that are directly applicable to CN research.

Selection of cultures for comparison is the most critical step for effectively establishing causation in cross-cultural studies. Although the comparison of a single Western with a single non-Western culture is common in cross-cultural psychology and CN studies, comparing at least three cultures, a pairing of which share the cultural variable of interest, and another pairing of which share an alternative explanatory variable (i.e. 'triangulation'), is needed to identify the cause of behavioral variation (Jahoda and Krewer, 1997; Medin and Atran, 2004). Without studying replicate cultures that share a feature of interest it is impossible to isolate which of the many differences between two cultures may be the cause of any observed between-group difference. Further cultural replication (beyond triangulation) and theory-driven rather than convenience-driven selection of cultures may also further limit the number of alternative explanations of cultural differences (Van de Vijver and Leung, 1997). For example, Kuhnen *et al.* (2001) found differences between two collectivistic (Malaysia and Russia) and two individualistic (Germany and US) cultures on their level of visual context sensitivity. By using two examples of each type of culture, they reduced the chance of detecting spurious differences between types, driven by unmeasured confounding variables. For example, an alternative explanation for visual context sensitivity is that it is related to use of a non-Roman alphabet. In this case, because Malaysians use the Roman alphabet while Russians use the Cyrillic alphabet, this alternative explanation was ruled out.

Another methodological strategy used in cross-cultural studies is to reduce inter-group variation by ensuring that subjects from different cultures are closely matched on demographic variables such as socioeconomic status (SES) and education level, as well as any elements of culture not directly under study (Van de Vijver and Leung, 1997; Schaffer and Riordan, 2003). For instance, Ji *et al.* (2000) reduce unwanted intergroup variation by comparing East Asian undergraduates attending college in the US to European American undergraduates in the same department. When it is impossible to match subjects on a demographic variable, the variable should be measured and used as a covariate in analyses (Van de Vijver and Leung, 1997).

Finally, valid cross-cultural studies are designed so that research stimuli are of equal familiarity and meaning to all subjects (Van de Vijver and Leung, 1997). A study by Yoon *et al.* (2004) illustrated the danger of not verifying cross-cultural equivalence of stimuli: only 22% of the 260 Snodgrass and Vanderwart (1980) line drawings of everyday objects, typically used for picture naming studies, showed both name and concept agreement between American and Chinese subjects. Language stimuli must also be translated effectively, and the characteristics of the test administrator and response procedures (e.g. computer use) must be of equal familiarity to all subjects (Van de Vijver and Leung, 1997).

Neural plasticity: mechanisms and methods

Cellular and systems level mechanisms of experience-dependent plasticity have been described in the neurosciences through the use of *ex vivo* molecular studies and *in vivo* studies in animals and humans. Because it is difficult to investigate cellular mechanisms of neural plasticity in humans, tissue culture and animal studies provide CN insight into the mechanisms and limits of neural plasticity that may underlie cultural differences, such as those described in the preceding section. Human neuroimaging studies of neural plasticity, on the other hand, provide an actual model for CN studies of cultural experience-dependent plasticity.

Two key cellular mechanisms of neural plasticity are long-term potentiation (LTP), which strengthens neural connections, and long-term depression (LTD), which weakens neural connections (Lynch, 2004). The long-lasting effects of LTP/D are thought to involve the morphological alteration of synapses such as the modification and generation of dendritic spines (Malenka and Bear, 2004). LTP and LTD likely occur in some form at every excitatory synapse in the mammalian brain (Malenka and Bear, 2004) and thus likely underlie neural plasticity induced by cultural experience.

The remarkable plasticity of the mammalian brain has been demonstrated by studies of animal sensory development. These studies have revealed that although genetic programs guide the development of neurobiological systems, normative sensory experience is critical in the development of functional neural circuitry (Knudsen, 2004). For instance, depriving young organisms of input from various sensory modalities including vision (Morishita and Hensch, 2008) and audition (Dahmen and King, 2007), results in profound functional disruptions of these systems. Following such major perturbations, large-scale reorganizations of sensory systems can occur, even cross-modally (Bavelier and Neville, 2002). For instance, Collignon *et al.* (2009) found that congenitally blind individuals recruit areas of visual cortex during auditory processing. Similarly, Ptito *et al.* (2008) found that blind Braille readers felt sensations in their fingers in response to transcranial magnetic stimulation (TMS) of occipital cortex. Such studies inform CN as to the range of possible plastic changes in the brain associated with different types of experience.

Learning experiences influence the brain throughout life, as exemplified by neural plasticity studies on human expertise. Although tissue and animal studies illustrate the range of the brain's plastic potential, studies of human expertise may be the most appropriate models for the study of cultural experience-dependent plasticity. Furthermore, studies of human expertise are typically conducted using neuroimaging techniques. Therefore, the methodological approaches in the following studies are most applicable to CN.

A prototypical example of human expertise is musical training (Münte *et al.*, 2002). Musical training influences auditory perception, motor performance, visuospatial processing, and interhemispheric processing (Stewart, 2008). These behavioral alterations are accompanied by structural alterations such as increased gray matter (GM) and white matter (WM) in primary auditory cortex, altered motor and somatosensory maps, and an enlargement of the anterior corpus callosum (Stewart, 2008). Structural brain changes are quantified using MRI and a number of structural analysis techniques including voxel-based morphometry (Ashburner and Friston, 2000) and cortical thickness measurement (Sowell *et al.*, 2001). Functional and structural changes related to musical training are often instrument- and effector-specific and are associated with the age of initiation of musical training even when years of musical experience are controlled for (for a review see Stewart, 2008).

Occupational specializations have also been associated with functional and structural neural plasticity including driving a taxi (increased GM in posterior hippocampus; Maguire *et al.*, 2000) and being a mathematician (increased GM in parietal cortex; Aydin *et al.*, 2007). Even short-term practice, such as learning to juggle, can result in structural changes (increased in GM volume in visual area MT and left intraperietal sulcus) evident after as little as 7 days of juggling training (Driemeyer *et al.*, 2008). Similar plastic changes were also seen in the brains of elderly individuals learning to juggle; however, changes in additional brain areas were seen as well suggesting that the nature of neural plasticity may change with age (Boyke *et al.*, 2008).

An important consideration in experience-dependant plasticity research is the potential contribution of genes to behavioral and neural variation. The young field of imaging genetics has begun to identify associations between common genetic variants, human cognitive functions and their neural correlates (Goldberg and Weinberger, 2004). Identified genetic polymorphisms associated with cognitive and neural effects are primarily those related to monoamine neurotransmitter receptors and transporters. For example genetic variation in the Catechol-O-methyltransferase gene (COMT) has been linked to variation in working memory and prefrontal cortex function (e.g. Caldú *et al.*, 2007). Similarly, genetic variation in the seratonin transporter gene has been linked to variation in anxiety related behavior and cingulate cortex-amygdala interactions (e.g. Pezawas *et al.*, 2005). Such genetic polymorphisms have been found in higher frequencies in certain regional groups (e.g. East Asians) than others (Benjamin *et al.*, 1996); therefore, it will be important for CN studies to consider the potential effects of such regional genetic variation on cross-cultural behavioral and neural differences.

METHODOLOGICAL GUIDELINES FOR CN

Methodologies from both psychology and neuroscience are directly applicable to CN studies. We have developed a set of eight guidelines for CN studies based on well-established methods from these parent fields. These guidelines concentrate on aspects of study design most different between other cognitive neuroscience imaging studies and CN: group selection, subject selection and stimulus selection. These design elements are especially important to the establishment of causation in CN because of the quasi-experimental nature of cross-cultural comparisons. The purpose of these guidelines is to allow CN researchers to fully capitalize on methodological approaches, both from cross-cultural psychology and cognitive neuroscience, which address challenges common to these fields and CN.

The first three guidelines relate to the selection of cultures for comparison:

(i) *Define and measure culture.* Culture should be clearly defined in the same way for all groups compared, not conflated with ethnicity or nationality, and measured using some form of acculturation scale (Van de Vijver and Leung, 1997). The measurement of cultural endorsement is especially important when studying individuals whose cultural heritage is different than their culture of residence (i.e. first or second-generation immigrants) as there is wide variation in which culture these individuals may endorse (e.g. Phinney and Devitch-Navarro, 1997).

(ii) '*Unpackage*' *culture.* In order to establish causation, culture should be deconstructed into psychologically relevant components. These components (e.g. individualism/collectivism) should be used to select cultural groups for comparison, and should be assessed in every study participant.

(iii) *Replicate cultures containing cultural element of interest.* In order to establish causality, at least three cultural groups must be compared, and further replication of cultures (i.e. more than three) is desireable (Jahoda and Krewer, 1997; Medin and Atran, 2004). Cultural groups should be selected that replicate the predicted causal cultural element. When such replication is not possible this should be considered during interpretation of results.

The next three guidelines refer to subject-specific elements of cultural groups selected.

(i) *Match or measure onset/amount of cultural experience.* Studies of human neural plasticity have demonstrated that both age at onset of experience and duration of experience are related to plasticity (Stewart, 2008). More specifically, Goh *et al.*, 2007 have demonstrated an interaction between aging and the influence of cultural experience on the brain and Park and Gutchess, 2006 have suggested that this type of interaction may be widespread. Therefore both age at onset of cultural experience and amount of experience should be measured and/or matched in CN studies. As in studies of animal and human sensory experience and human expertise, there may be a sensitive period for the impact of cultural experience on the brain.

(ii) *Consider the effects of regional genetic variation.* Regional genetic variation has been shown to have measurable effects on the brain and behavior and genetic heritage and culture are often counfounded (Benjamin *et al.*, 1996; Goldberg and Weinberger, 2004); therefore, in order to make inferences about the relative contributions of genetics and cultural experience to cross-cultural neural differences, comparison groups with shared genetic heritage but differing cultural experience should be included. For instance, a study investigating the neural basis of individualism/collectivism differences in Chinese and European American subjects could also include a third generation or later Chinese American group. If cross-national differences in IC are driven by culture, the European American and Chinese American group should be more similar to each other on the dependant neural measure than to the Chinese group, whereas if cross-national differences are driven by regional genetic variation, the Chinese and Chinese American group should be more similar to each other than to the European American group. Alternatively, participants could be genotyped at loci known to be related to the cognitive function under study.

(iii) *Match groups.* Factors other than the cultural element of interest should be matched between groups or measured and included as covariates in the analysis when matching is not possible (Schaffer and Riordan, 2003; Van de Vijver and Leung, 1997).

The final two guidelines concern characteristics of the experimental stimuli used.

(i) *Equate stimuli.* The equivalence of the experimental stimuli for all cultural groups under study should be verified (Van de Vijver and Leung, 1997). Equating stimuli may involve group-specific adjustments to stimuli.

(ii) *Equate performance.* In order to disassociate neural and behavioral differences, task performance between groups should be equated as closely as possible (Price and Friston, 1999). Equating performance may also require group-specific adjustments to stimuli.

LITERATURE REVIEW RELATIVE TO GUIDELINES

Literature review: selection of studies. We have selected seventeen studies from the literature for inclusion in our review. These studies are summarized in Table 1. Our goal was to provide a picture of the nascent field of CN and to compare the extant CN literature against our methodological guidelines derived from cross-cultural psychology and cognitive neuroscience. In order to limit the scope of our review and ensure studies are maximally comparable, we have only included neuroimaging studies that compare at least two cultural (or national/linguistic) groups exposed to the same or equivalent stimuli. Based on these criteria, we have excluded some studies important to the field of CN: cultural priming studies in bicultural individuals (Sui and Han, 2007; Lin *et al.*, 2008) and studies that compare two cultural groups exposed to culturally familiar and unfamiliar stimuli, such as studies of cross-cultural music perception (Morrison *et al.*, 2003; Nan *et al.*, 2008). While the contributions of such studies are valuable to CN, methodological differences between these studies and those included in this review, especially the lack of two comparison groups in the case of cultural priming studies, would have made comparison against our guidelines less meaningful. However, it is important to note that cultural priming studies avoid some of the methodological challenges related to group matching that our guidelines address, and in this way make a unique and important contribution to CN research.

For our literature search we relied primarily on PubMed and Google Scholar using the search terms ‘cultural, cross-cultural, brain, neuroscience, neuroimaging, cognition and perception’. We also identified studies from the citations of other collected studies and the ‘related articles’ feature on PubMed. Selected studies cluster in three broad domains of cognition: language, perception, social cognition. We have evaluated each of the included studies relative to our guidelines and indicated whether each guideline was met, partially met or not met in Table 1. In the following section we discuss each guideline in terms of the current CN literature and provide an example of a study that met that guideline particularly well. Criteria for partially meeting each guideline are also outlined below.

Guidelines with case studies

(i) *Define and measure culture.* A study could partially meet this guideline by clearly defining culture the

Table 1 Cultural neuroscience studies compared to our guidelines derived from cross-cultural psychology and cognitive neuroscience

Citation	Meth.	Task	Nationality	Language	Define 1	Unpackage 2	Replicate 3	Years/onset 4	Genetics 5	Eq. Groups 6	Eq. Stimuli 7	Eq. Perfor. 8
Language												
(Paulesu *et al.*, 2000)	PET	Word reading	UK (London), IT (Milan)		P	P	N	Y	N	P	Y	N
(Kochunov *et al.*, 2003)	MRI	None	CN, US	CN, EN	P	P	N	N	N	Y	A	A
(Valaki *et al.*, 2004)	MEG	Word listening		CN, EN, SP	N	P	P	N	N	P	Y	N
(Bolger, *et al.*, 2005)	PET, fMRI	Word reading(Meta)		EN, FR, GM, IT, JP, CH	P	P	Y	A	N	P	P	A
(Tang *et al.*, 2006)	fMRI	number reading	CN, (US, UK, CA)	CH, EN	N	P	P	N	N	P	Y	N
Visual												
(Grön, *et al.*, 2003)	fMRI	Visual memory	CN, Caucasian		N	P	N	N	N	P	P	Y
(Gutchess, *et al.*, 2006)	fMRI	Visual scene processing	CN, US		P	P	P	P	N	Y	P	Y
(Goh *et al.*, 2007)	fMRI	Visual scene processing	US, SN		P	P	N	N	N	P	P	P
(Hedden, *et al.*, 2008)	fMRI	Frame line illusion	East Asia, US (Western Euro.)		N	P	N	P	N	Y	P	Y
(Lewis, *et al.*, 2008)	ERP	Visual odball task	US (European or Asian)		P	Y	N	Y	P	Y	Y	P
Social												
(Moriguchi *et al.*, 2005)	fMRI	Expression viewing	JP, Caucasian		N	N	N	Y	N	P	P	N
(Kobayashi, *et al.*, 2006)	fMRI	False belief task	JP, US	(JP and EN), EN	p	P	N	N	N	P	P	Y
(Hot, *et al.*, 2006)	ERP	Expression viewing	JP, FR		P	P	N	Y	N	P	Y	Y
(Zhu, *et al.*, 2007)	fMRI	Self/other, trait judgment	(UK, US, AU, CA), CN	EN, CN	N	P	P	Y	N	Y	P	P
(Kobayashi, *et al.*, 2007)	fMRI	False belief task	JP, US	(JP and EN), EN	P	P	N	N	N	Y	Y	Y
(Chiao *et al.*, 2008)	fMRI	State/trait self judgments	JP, US (Caucasian)		P	Y	N	Y	N	P	Y	Y
(Han *et al.*, 2008)	fMRI	Self/other, trait judgment	CN	Christian, Non-religious	Y	P	N	P	N	Y	Y	P

Task column: only task of interest (not control) is represented. Nation column: the following abbreviations are used: CN = China, US = United stated, SN = Singapore, JP = Japan, FR = France, UK = United Kingdom, AU = Australia, CA = Canada, IT = Italy. Langauge column: The following abbreviations are used: JP = Japanese, EN = English, CN = Chinese, SP = Spanish, FR = French, GM = German, IT = Italian. Guidelines: N = not met, P = Partially met, Y = fully met, A = not applicable.

same way for all groups; however, to fully address guideline 1, the definition of culture could not simply be a nation or language, and culture, as defined, must have been measured in all participants. The only study to fully meet this guideline, Han *et al.* (2008), compared Christian to non-religious Chinese adults. The religious attitudes and religious knowledge of both groups were measured and the Christian group was found to be higher than the non-religious group on both measures. Though Han *et al.* (2008) employ a narrow definition of culture (religion), a similar strategy for definition and measurement can be used with broader, more typical designations of culture. Many of the studies we considered defined culture as either a nation or a language despite the fact that there often is not a one-to-one relationship between language and/or nationality and culture. Culture was also commonly defined as a multi-national group such as East Asian or Western, implying that these broad groups are culturally homogeneous, which is only true at the most superficial levels of analysis. Finally, a number of studies defined culture in different ways for different groups, e.g. Japanese compared to Caucasian. All of these group selection strategies can result in comparing non-equivalent groups, making interpretation difficult or meaningless. Thus, properly defining culture will be critical for future CN studies.

(ii) '*Unpackage*' *culture*. Any study that mentioned specific cultural elements rather than 'culture' alone, while describing the research question or explaining the findings was considered to partially satisfy Guideline 2. Only studies that measured the cultural variable of interest in both groups and used these measurements in the ensuing analysis fully addressed this guideline. Chiao *et al.* (2008) fully met this guideline by measuring IC in their subjects and regressing this variable against fMRI data on a self/other judgment task. Although Chiao *et al.* (2008) also found correlations with IC in their data, culture (whether participants where Japanese or American) was not correlated with IC, suggesting the need for caution when selecting possible explanatory cultural variables. Only one other study, (Lewis *et al.*, 2008), fully met this guideline by measuring the cultural variable of interest (IC) and using it in their analysis. Future CN studies will contribute more to our understanding of the relationship between culture and the brain by not only unpackaging culture but measuring how specific cultural elements relate to their dependant neural measure.

(iii) *Replicate cultures containing cultural element of interest*. Studies could partially satisfy this guideline by including more than one group with a given cultural element of interest. To fully meet Guideline 3 a study must have included at least two cultures representing each cultural element of interest in sufficient numbers that these groups could be analyzed separately. A meta-analysis of word reading studies in Western alphabetic languages compared to word reading studies in Eastern logographic languages was the only study to fully meet this guideline (Bolger *et al.*, 2005). By comparing multiple cultures that shared orthography but differed in other ways, the authors were able to specifically identify neural regions that related to orthography rather than other elements of language or culture. Although replication in CN studies is logistically challenging and costly, replication is crucial for identifying an explanatory variable more specific than 'culture'. Such replication may be accomplished though meta-analyses such as the one above or multi-site collaborations such as the study by Henrich *et al.* (2005) exploring economic decision making behavior in 15 small-scale societies.

(iv) *Match or measure onset/amount of cultural experience*. Studies that mentioned and roughly matched the amount of cultural experience typical of each study group partially met this guideline. However, only studies that tested subjects within their native cultures fully met Guideline 4. Chiao *et al.* (2008) met this guideline in a novel way by conducting fMRI scans of subjects residing in their native cultures (Japanese or American) and then comparing these scans (from two different scanners) directly. Because cross-scanner comparison is difficult due to scanner-specific artifacts in the data, the methods of cross-scanner comparison described in Chiao *et al.* (2008) will be useful for future CN studies. Unfortunately, none of the studies considered included individuals with different amounts and different ages at onset of cultural experience, (e.g. subjects who came into their culture of residence at different ages) and/or used onset or years of cultural experience in their statistical analyses. However, given that age of onset is a powerful mediator of neural plastic changes resulting from expertise (Stewart, 2008), this strategy may be useful in determining whether a sensitive period exists for the neural influences of cultural experience.

(v) *Consider genetics*. A study that included at least one group in which culture and genetic heritage were not completely confounded could partially satisfy guideline 5; however, in order to fully meet Guideline 5, and be able to make inferences about cultural versus genetic effects, a study had to include a separate group with cultural experience similar to one comparison group and genetic heritage similar to that of the other. Lewis, Goto and Kong (2008) was the only study to even partially satisfy this guideline. They compared mono-cultural European Americans to bi-cultural Asian Americans and measured each subject's level of individualism and collectivism (treated independently). By including level of cultural endorsement in regression analyses with event-related potential (ERP) data, they were able to determine that the level of collectivism mediated the relationship between an ERP component and culture, suggesting that the collectivism component of culture rather than genetic factors—which likely did not vary with IC—was driving their ERP group difference. Although disentangling the influence of genetic and cultural factors on brain function requires the inclusion of additional control groups, attention to the potential influence of regional genetic variation in CN studies will greatly enhance the information CN may contribute to the nature/nurture debate.

(vi) *Match groups.* Studies that considered basic elements of group matching such as age and handedness (important for neural lateralization) partially addressed this guideline. Only studies that measured additional neuropsychological variables relevant to the study topic, such as IQ or reading ability, and verified group matching by direct statistical comparison, fully addressed this guideline. Gutchess *et al.* (2006) provide a particularly good example of group matching; the authors not only matched groups on age, education level, and culturally-appropriate questions of world knowledge (Wechsler Adult Intelligence Scale information subtest), but also two visual speed of processing tests relevant to the visual scene processing task under investigation. In this way, the authors were able to rule out alternative explanations of group differences based on general demographics and cognitive skills tangentially related to the task. More than half of the studies considered compared groups matched only on basic demographic criteria such as handedness; however, given the nature of cross-cultural comparison, additional group matching measures, beyond those typically employed in cognitive neuroscience studies, are necessary for unambiguous interpretation of between-group differences.

(vii) *Equate stimuli.* Tasks that partially met this guideline made some attempt to equate stimuli for both groups or used tasks simple enough to reasonably assume cultural equivalence. Only studies that verified stimuli equivalence for all groups fully satisfied this guideline. For instance, Hot *et al.* (2006) used emotional stimuli whose emotional valence ratings had been previously normed in both comparison groups (Japanese and French). Similarly, Paulesu *et al.* (2000) designed their word reading task using words that were among the 7500 most common in both language groups compared. Unfortunately, about half of the studies considered did not verify stimuli equivalence across comparison groups and/or acknowledged substantial differences in stimuli meaning across comparison groups.

(viii) *Equate performance.* Studies partially met this guideline if they measured performance and it was at least partially equivalent across groups. Fully meeting this guideline required that all measured aspects of performance were equivalent across groups. Kobayashi*et al.* (2006) measured both accuracy and reaction time on their false belief task and found no group differences on either measure. In general, attendance to performance matching was mixed among the studies. Stimulus and performance matching will be especially important for future CN studies because these strategies reduce the number of possible explanations of between-group differences, which are especially high during cultural comparison.

Overall many studies in CN are already unpackaging culture (ii), matching groups (vi), using culturally equivalent stimuli (vii) and matching performance (viii). Future consideration of these guidelines will further aid in the interpretation of the inherently complex results of CN studies. Fewer studies are currently defining and measuring culture consistently (i), replicating cultures sharing a cultural element of interest (iii), matching the amount of cultural experience across groups (iv), and disentangling culture and genetics (v). It should involve relatively little effort for future CN studies to improve the consistency of their cultural definitions and reference to the anthropological and psychological literature should aid in cultural definition improvement. However, studying individuals immersed in their own cultures by performing multi-site imaging studies (iv) and increasing the number of study groups in order to rule out alternative genetic and cultural explanations of between-group differences (v) will require future studies to employ larger and more complicated designs. Additionally, only one study considered here performed brain structural analyses as opposed to functional analysis only (Kochunov *et al.*, 2003). Given the structural brain changes seen in studies of human expertise, future CN research will benefit from including structural as well as functional analyses.

CULTURE AND NEUROSCIENCE: ADDITIVE *AND* SYNERGISTIC

Considering the contributions of parent fields to CN, current CN studies, and potential future contributions of CN research we conclude that the combination of culture and neuroscience is both additive and synergistic. Cross-cultural psychology and cognitive neuroscience contribute concepts to CN in an additive fashion. (i) The cultural variations in behavior identified by cross-cultural studies in psychology provide avenues for neuroscientific inquiry. (ii) Cross-cultural psychology and psychological anthropology theory provide useful background and testable hypotheses for CN to explore. (iii) The molecular and systems level mechanisms of neural plasticity identified in animal studies inform CN as these mechanisms also likely underlie neural plasticity that results from cultural experience. (iv) Finally, neuroimaging studies of the effects of expertise on the human brain provide a conceptual and methodological model for CN studies. Cross-cultural psychology and neural plasticity studies in cognitive neuroscience also additively contribute methodologies to CN, as demonstrated in our guidelines. Translational methodologies form parent fields will enhance the explanatory power of CN research. Some of the findings of CN research will also be additive, reflecting a direct union of information from parent fields. For example, neuroimaging will associate brain areas with known cross-cultural differences, and CN research will provide additional evidence of neural plasticity in the human brain.

Culture and neuroscience also have the potential to be truly synergistic; some of the findings of CN may be fundamentally different form those in cross-cultural psychology and neural plasticity research to date. Unique information about the mechanics of human neural plasticity may arise from studying the effects of differential cultural experience on the brain, as cultural experience has properties that differ from expertise and other types of experience previously studies in humans: it is widely shared, not self-selected, socially transmitted, constantly evolving and it influences many cognitive and sensory domains. Additionally, because culture is not self-selected, as expertise in a musical instrument or sport is, it may be easier to tease apart the effects of cultural experience from internal sources of neural variation.

The synergy of cross-cultural studies and neuroscience also holds the potential to reveal some truly novel information about cross-cultural differences in behavior. As in the example of cross-cultural color terminology (Abramov and Gordon, 1994), the physiology of the nervous system constrains variation in human behavior to some extent. Studying the neurobiological basis of cultural variation may help explain the patterns of cross-cultural behavioral variation described in psychological and anthropological studies. Alternatively, just as Boas (1896) noted that cross-culturally similar aspects of behavior can have different historical and environmental causes, they may also have different neural underpinnings. For instance, Grön *et al.* (2003) found that despite equivalent performance on a nonverbal episodic memory task, Caucasian subjects relied more on the ventral visual stream and Chinese subjects relied more on the dorsal visual stream for neural processing.

Despite the potential novel contributions of CN research, the combination of culture and neuroscience results in some unique logistical challenges. These challenges include cultural differences in the rate of age-related changes in the blood oxygen level dependent (BOLD) signal, differences in brain size and shape, and, most notably, limited availability of non-invasive measures of brain function in different cultures (Park and Gutchess, 2002). Many of the neuroimaging modalities most appropriate for studying CN questions, such as functional magnetic resonance imaging (fMRI), positron emission tomography (PET), and magneto encephalography (MEG), are not portable and not widely available for research purposes in close proximity to all cultural groups of interest (Han and Northoff, 2008). Even when neuroimaging methodologies are available locally, the individual characteristics of each imaging device make cross-device comparisons difficult, though feasible with careful matching of hardware and software, (Sutton *et al.*, 2008). Therefore, although exciting discoveries in CN have already been made (Han and Northoff, 2008), the full potential of CN research will be reached through a combination of international collaboration, translational methodologies from parent fields, and the further development of new methodologies that address the unique challenges of CN studies such as portable imaging technologies and cross-scanner data comparison.

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