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REVIEW ARTICLE

Integrating culture-as-situated-cognition and neuroscience prediction models

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Abstract The interface of mind, brain, culture, and behavior has provided rich ground for speculation, theorizing and empirical research. To date, theorizing has focused on between-country difference and much research has focused on quasi-experimental design in which groups are compared and the reasons for found differences imputed to be about the culture-brain interface. The authors of this paper argue for a somewhat different approach. We conceptualize culture as a set of human universals that are dynamically triggered in context. In doing so we integrate culture-as-situated-cognition (CSC) and neuroscience prediction (NP) models to yield a number of novel predictions: first, all societies include cues triggering both individualistic and collectivistic mindsets. Second, whether a mindset is triggered by a particular cue and what a triggered mindset implies for judgment, affective and behavioral response depends on spreading activation within the associative network activated at that moment. Third, universal features of culture are likely necessary from an evolutionary perspective; societies develop and sustain specific instantiations of these universals whether or not these particular instantiations were ever optimal, simply because they are the way 'we' do things. The CSC–NP model explains why models that assume fixed differences do not always find behavioral

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differences; effects are probabilistic, not deterministic. It also explains why models that assume that particular cultural practices are functional are unlikely to be supported. We review extant studies that combine neuroscientific and priming methods and highlight what needs to be done in future studies to address gaps in current understanding of the mind–brain–culture–behavior interface.

Keywords Cultural neuroscience · Priming · Individualism · Collectivism · ERP · fMRI

What is the interplay between brain function and culture? A burgeoning literature in cultural neuroscience (CN) has focused on a variety of specific formulations which taken together focus attention on a particular set of ideas (e.g., Cheon et al. 2013; Kitayama and Uskul 2011). These ideas point to the possibility that the brain–culture interface is structure-based, deeply rooted, and essentially fixed, resulting in a particular patterning of norms, values, behaviors, and brains. This literature has not yet begun to focus sufficient attention to the other possibility, which is that the brain–culture interface is situated and dynamic, based on functional networks that are both universal and dynamically constructed from situational cues. The first possibility is simple to grasp, well instantiated in the current literature, and based on a reading of culture as being mostly about between-society difference. Unfortunately this formulation misses both those aspects of culture that are human universals and those aspects of culture that are quite particularistic. The second possibility is based on a reading of culture as being mostly about between-society commonalities in universal processes that are idiosyncratically particularized. In the current paper, we suggest that this latter possibility is well suited for research at the mind–brain–culture–behavior interface and outline what is to be gained by integrating this situated approach into neuroscience research.

Cultural and cross-cultural research highlights both that each society develops a distinct culture and in that sense is unique and that societies can be categorized by general cultural patterns, often termed individualism and collectivism (or alternatively analytic and holistic or independent and interdependent). Societies are assumed to differ in the centrality of individuals, as exemplified by contrasting opposing societal infrastructures in which individuals are conceived as central, with groups playing a peripheral role to those in which groups are central, with individuals playing supporting roles (Hofstede 1980; Oyserman et al. 2002; Triandis 1989). Consequences of these core differences are thought to extend to how the self is organized (hence the terms independent and interdependent self) and how thinking generally proceeds (hence the terms analytic and holistic). Current work in CN focuses on these general cultural patterns, which are assumed to influence brain processing so that people socialized in a culture have stable culture-specific brain structures (e.g., Gutchess et al. 2010; Hedden et al. 2008; Kitayama and Park 2010; Tang et al. 2006). In line with this assumption, CN research has focused on documenting regions of the brain associated with processing information about the self and documenting between-societal differences in whether particular tasks are associated with activation in these regions (e.g., Han et al. 2008; Kitayama et al. 2009; Zhu et al. 2007).

While yielding a large and productive program of research, this formulation gives short shrift to the other possibility, which is that elements of individualism and collectivism are prevalent in all societies and that what differs is not whether individualism and collectivism exist, but when and in what circumstances individualism and collectivism come to mind and influence one's self-concept, thinking, feeling, and behaving. In the current paper we focus on this possibility. To do so we integrate culture-as-situated cognition (CSC, e.g., Oyserman 2011, in press) and neuroscience prediction (NP, e.g., Bar 2009; Clark 2013; Friston 2009) models to predict that societies are both similar, sharing a set of universal cultural processes, and distinct, each with its own very particular practices. The idiosyncratic ways that these universals have been operationalized in each society are imbued with meaning, become the way that 'we' do things and hence have inertial tendencies to remain stable. This paper is comprised of four sections: summaries of the CSC and NP models, a description of the novel hypotheses yielded by our integration of the CSC and NP models, and a summary of how the elements of our integrated model have been tested in CN research to date. We end highlighting gaps to be addressed in future research.

The culture-as-situated-cognition (CSC) model: culture as universal and particularized

We start with the premise that humans need other humans to survive and that sticking together is both vital and problematic (Boyd and Richerson 1985; for a detailed discussion see Oyserman 2011, in press). Culture is a solution to the problems that arise from sticking together. These include managing relationships to minimize dangerous conflict, clarifying group boundaries so that resources can be shared with in-group members and out-group members can be exploited, and facilitating individual innovation so that the group can develop and not stagnate. The first two of these cultural universals highlight what has been termed collectivism, a focus on how one fits into a relational (and hierarchical) structure and a focus on group membership as a central feature. The third of these cultural universals highlights what has been termed individualism, a focus on individual initiative and unique attributes. While cultural psychologists often contrast individualistic and collectivistic societies, our analysis implies that across societies, human cultures universally include both elements of individualism and of collectivism. Simply contrasting societies as a way of studying culture is insufficient because it only allows for testing between-society difference and does not allow for testing either the consequences of either the universal or the particularized elements of culture (a detailed analysis can be found in Oyserman 2011).

The CSC model integrates situated cognition and associative processing literatures (Anderson and Bower 1973; Anderson 1983; Neely 1977) to highlight how cultural processes are both universal (the same across societies) and particular (requiring knowledge of specific practices within a society) (Oyserman 2011;

Oyserman and Lee 2008; Oyserman and Sorensen 2009). Central to the CSC model is the notion of cultural mindsets, which are cognitive schemas including mindset-relevant content, procedures, and goals linked in associative networks (Oyserman et al. 2009). Following the presumed universality of core elements of human culture, the CSC model assumes that societies universally socialize their members to both be sensitive to relationships and group-boundaries and to be sensitive to chances to try something new (which means doing their own thing and sticking out) in at least some situations. In Fig. 1 we show this distinction by showing the process for two societies, Society 1 and 2.

Over time, the particular situations or features of situations in which relationality is relevant become associated with other aspects of relationality in memory. In the same way, the particular situations or features of situations in which group boundaries are relevant become associated with other aspects of group boundaries in memory, and the same for the particular situations or features of situations in which trying something new is relevant. The result is a set of associative networks of knowledge, such that activating one element of the network probabilistically activates other elements through spreading activation. This is depicted graphically in Fig. 1 in the second row as a set of specific cues, practices particular to a specific society, that activate particular memories and knowledge structures. Both Society 1 and 2 have situations linked to elements associated with individualism and collectivism. These elements are depicted as circles and triangles of varying hues to distinguish specific elements that might be available in memory in societies considered individualistic (circles) and collectivistic (triangles).

The notion that these elements activate other elements through spreading activation is depicted with arrows interconnecting the geometric forms. As can be seen in Fig. 1, the process is probabilistic, whether an individualistic (or collectivistic) mindset is primed by a particular activated element depends in part on how it was cued and what else was accessible at the same time. This probabilistic formulation fits modern formulations of associative processing and its effects on which of all available information is accessible and interpreted as relevant at the moment of judgment (e.g., Bargh 1996; Higgins 1996; Schwarz 1995) and is based in the classic formulations of Anderson (1983), Collins and Loftus (1975), and Wyer and Carlston (1984). By activating cultural mindsets, everyday situations can have downstream consequences on thinking, feeling and doing. Effects can occur in domains that are quite distal from cultures' development as a way to handle the problems of sticking together.

Mental representations, whether of ideas, events, experiences, or knowledge of practices, goals and procedures, once formed are assumed to be interconnected in associative networks, in which each element is represented as a node and connections represented as links. Nodes (e.g., specific bits of knowledge) derive their meaning from how they are made sense of when they come to mind. What a node likely means comes from its place within the network of interconnections so that what else comes to mind when the node comes to mind dynamically creates a particular meaning. Nodes that are frequently cued at the same time develop strong (direct) associations; nodes that are less frequently cued at the same time will have weaker (less direct) associations. Hence, what something means will depend both on

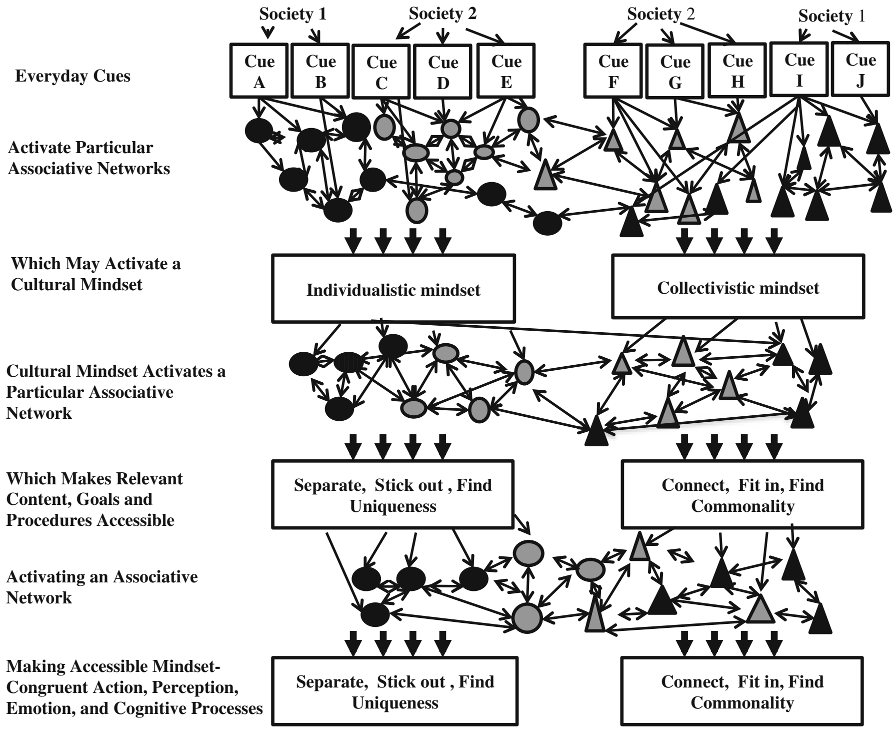

Fig. 1 The culture as situated cognition (CSC) model. The CSC model articulates a probabilistic understanding of the brain–culture interface. Because processing is fundamentally associative, whether an initial cue results in a predicted response is highly dependent on the associations that come to mind at each stage. This process is modeled for two societies, labeled *Society 1* and *2*. Starting at the top row, the CSC model proposes that each society includes everyday cues associated with both individualism (*cues A–E*) and collectivism (*cues F–J*). These cues activate associative networks that are specific to the particular society (*row 2*, presented as *circles* and *triangles* of *different color*s). A cue activates a node and that node activates others through spreading activation. Each node is a specific memory, on-line interpretation, or action. A cue can activate an individualistic or a collectivistic mindset directly or indirectly through spreading activation, shown the *single* and *two headed arrows* (*row 3*). Once a cultural mindset is activated, it cues an associative network (*row 4*, again presented as *circles* and *triangles* of *different colors*) that makes mindset-congruent content, goals, and procedures accessible directly or indirectly through spreading activation (*row 5*). The resulting activation of congruent associative networks (*row 6*) increases the likelihood of mindset-congruent actions, perceptions, emotions, and cognitive procedures (*row 7*). Effects are probabilistic, depending on spreading activation, so that starting with a cue (*A–J*) likely leads to cuing an individualistic or collectivistic mindset, but the effect is probabilistic rather than certain. The same probabilistic principle applies to the consequences of activating a mindset for action, perception, emotion, and cognition. (Color figure online)

what usually comes to mind at the same time and on what recently came to mind in that particular situation. It is likely that some elements that are more strongly associated with one universal aspect of culture (e.g., how relationships work) are also weakly associated with another universal aspect of culture (e.g., distinguishing in from out-group or doing one's own thing and novel solutions to common problems). In this way, and as also shown by the interconnected geometric forms in

Fig. 1, it is likely that constructs of various associative networks are interconnected in some ways, making it possible to shift between associative networks. While there is variation across societies in the likelihood that individualistic or collectivistic mindsets are accessible at the moment of judgment, both mindsets seem available in both modern (see for a meta-analysis of developed societies, Oyserman and Lee 2008) and traditional (see for examples in non-developed societies, (Cronk 2007; Cronk and Leech 2012) societies.

Taken together, the CSC model predicts that all societies include elements of individualism and collectivism, and that these elements are associated with particular referents in each society. While *how* individualism and collectivism are concretely embodied in a society is particular to the mores of that society, societies are not predicted to differ in *whether* they contain the kind of cues that can activate an individualistic mindset or the kind of cues that can activate a collectivistic mindset—that is universal. Once a collectivistic mindset has been cued, associative networks activated include content, procedures, and goals relevant to collectivism. Once an individualistic mindset has been cued, associative networks activated include content, procedures, and goals relevant to individualism. Collectivistic mindsets cue connecting and relating procedures while individualistic mindsets cue separating and pulling apart procedures (Oyserman et al. 2009). The model does not assume that particular practices are necessarily functional within a society, rather that once instantiated, they become the way that 'we' do things, and thus resistant to change (see also, Cheon et al. 2013; Lindenbaum 2008).

Figure 1 provides a simplified version of the CSC model that concretizes the interplay between the particular and the universal in the following way. First, societies can differ in their everyday cues but not in whether they have cues that activate both individualistic and collectivistic mindsets. This is denoted in the Figure by the link between Society 1 and cues A, B, I, and J and between Society 2 and cues C, D, E, F, G, and H. Second, cues differ in location within the associative network and in their likelihood of directly or indirectly activating a cultural mindset. As denoted by the length of the path from each cue to the cultural mindset box in the next row of Fig. 1, some cues are likely to activate a cultural mindset quite directly. Other cues are associated with a cultural mindset only indirectly or are included in associative networks linked to both cultural mindsets so their effect on salient mindset is contingent on what else is activated at the same time. This highlights the probabilistic nature of cultural mindset effects. Thus for example, rather than assume that collectivists always reason by seeing wholes and connections and that individualists always reason by seeing parts and unique elements, our culture as situated cognition approach highlights that thinking is both situated and pragmatic. Reasoning depends on what is cued in the moment. Depending on the point of entry, an associative network can yield different results, at least some of the time.

Evidence that individualistic and collectivistic mindsets are universal

Supporting the notion that cultural mindsets are universal, a meta-analytic review of the 'culture priming' literature (Oyserman and Lee 2008) replicates the size and direction of average between-societal differences in content of self-concept, values, and relationality found in a prior meta-analytic review (Oyserman et al. 2002). A variety of simple techniques can be used to prime cultural mindset. For example, just as people from societies described as collectivistic use more relational and group markers to describe themselves than do people described as individualistic (Oyserman et al. 2002), so do people who describe themselves after first circling first person plural pronouns in a text (Oyserman and Lee 2008). A variety of cues have been demonstrated to have this effect and the effect is bidirectional—shifting response from individuals socialized in societies described as either individualistic or collectivistic. In addition to circling first person singular (versus plural) pronouns (Gardner et al. 1999), describing differences (versus similarities) between oneself and one's family and friends (Trafimow et al. 1991), speaking in English versus Chinese in contexts that make one or the other feel natural (Lee et al. 2010), gesturing with one finger versus two linked fingers (Arieli et al. 2014), and other situated primes (Mourey et al. 2013) all increase self-focus.[1]

Downstream consequences of having a salient individualistic and collectivistic mindset have also been found. For example, while initial research highlighted between group-differences in cognitive focus, with East Asians more frequently processing contextual information than Americans (e.g., Ji et al. 2000; Kitayama et al. 2003; Masuda and Nisbett 2001), more recently studies have documented that participants from these and other groups can be made to shift their attentional focus. Thus, European American, Chinese, Hong Kong Chinese, Korean, and Norwegian participants were better at ignoring context after being primed with individualism and better at paying attention to relationships after being primed with collectivism (Kühnen and Oyserman 2002; Lin and Han 2009; Oyserman et al. 2009). These studies employ an array of dependent variables demonstrating basic perception and recall effects. Effects are found for dichotic listening and Stroop tasks, in which performance is improved by ignoring extraneous background information. They are also found for visual perception and recall tasks, in which performance is improved by paying attention to relationships, as well as for Navon tasks, in which performance is improved by the match between salient mindset and processing. Effects on basic processing translate to different responses to everyday situations. For example, people primed with a collectivistic mindset perceived more relationships among objects and this influenced their willingness to purchase elements that seem to complete a set (e.g., a case to go with a cellphone) and willingness to pay more to do so (Mourey et al. 2013). Importantly, these effects are found whether the cultural mindset prime is well established (e.g., pronoun circling) or novel (e.g., manipulating the Amazon logo). By demonstrating that priming individualistic versus collectivistic mindsets cues the same mental processes across

[1] While no single prime should be assumed to fully operationalize cultural mindset to the exclusion of other related constructs, by triangulating across priming methods, it is possible to begin to more concretely address causal processes and to understand their overlap with other related constructs. This triangulation process is not possible when using between group comparisons instead of priming. Differences can be described as fitting predictions but there is no possibility of triangulating and testing whether found differences are due to culture or to something else. The comparison in and of itself is mute as to the appropriate interpretation, leading to open questions about what is meant by a cultural analysis—is culture the same as social class, is social class the same as educational attainment, can one society substitute for a whole group of societies, and so on.

societies which otherwise differ, these studies provide evidence for cultural universality within very different societies.

Evidence that cultural knowledge is particularistic

Yet culture is more than universal processes of individualism and collectivism. It also involves a very particular framework of expertise, knowing what to do, how to proceed, and what things mean in a particular society, time, and place. For example, researchers have shown that color, smell, posture, and gestures such as a "thumbs-up" gesture carry no meaning or a different meaning, depending on the society. Colors, including hue and saturation are associated with different objects in different cultures and affective response to a color in a particular hue and saturation depends on its specific associates within the culture (Palmer and Schloss 2010; Palmer et al. 2013). Standing up straight can be associated with honor, but not always (IJzerman and Cohen 2011). A thumbs-up gesture implies approval and optimism in many Western societies, but hostility in some Middle Eastern societies (Archer 1997; Chandler and Schwarz 2009). Saying that something smells fishy means that it is suspicious if one is speaking English, but fish and suspicion are not linked in an array of other languages (Lee and Schwarz 2012). As these examples of cues and symbols demonstrate, being embedded in a culture provides expertise.

Being embedded in a culture also provides a broad set of implicit expectations and explicit rules about what has meaning and value and what should likely occur in a variety of everyday situations (Oyserman 2011). For example, living in a culture implies knowing prosaic things like whether today is a holiday and what lunch entails. Consider lunch, is a lunch break expected? If so, how long is the break? When does it occur? The same holds for holidays; if today is a holiday, does that mean shops are open or closed? Indeed, in a series of experiments involving participants in Hong Kong and the US, Mourey et al. (2014) demonstrated the consequences of cultural fluency (things occur as expected) and cultural disfluency experiences. As predicted, experienced cultural disfluency (ambiguous mismatch between prediction and experience) resulted in shift to processing systematically (Mourey et al. 2014). Living in a culture also implies knowing the rules. Tighter societies have more rules, and more strictly enforced rules about which behaviors are permissible in a variety of situations (Gelfand et al. 2011).

Summary

In summary, the CSC framework clarifies how cultural processes can be both universal and particular and posits that these processes have downstream consequences for one's thoughts, feelings, and actions. If thinking is for doing and what people do is context-dependent, the mind is both a cultural tool and a cultural product. If thinking occurs in the brain, then the influence of cultural processes on cognition, emotion, and behavior involves the brain. In the next section we briefly summarize neuroscience prediction models highlighting their interface with the CSC formulation of cultural as both a universal and a set of particularistic processes.

(Social) Neuroscience prediction models

In this section we consider general and social neuroscience prediction models and the implications of these models for the CSC formulation of cultural universal and particularistic processes. We start with the three universal cultural elements (recognizing one's in-group, following relationship rules, and innovating where necessary and permitted) and highlight their parallels in neuroscience models. Each of the cultural universals is social in nature—they occur in social contexts and they involve both learning about others ('who is in my group', 'what are *our* rules') and from others ('I could copy that guy's innovation') as well as understanding the self. Social neuroscience focuses on each of these elements (Adolphs 2009; Lieberman 2007). Where in the brain these processes are instantiated is well documented. Specifically, a core organizational principle in the social brain is the distinction between mental and physical information. Processing of one's own and others' internal mental states relies on medial brain areas (i.e., medial prefrontal and medial parietal cortex), whereas processing of social information that does not involve mental states relies on lateral brain areas (i.e., the posterior superior temporal sulcus and somatosensory cortices) (Lieberman 2007).

A universal need to fit in and connect

Given that sensitivity to others and the need to fit in and connect with in-group members are assumed to be fundamental, people should really care about being connected to and not being rejected by others, care about their social reputation, and whether they are being treated fairly by in-groups. Indeed, the neural circuitry involved overlaps with the neural circuitry for basic signals for survival (Fareri and Delgado 2014). Thus, social pain of rejection and unfairness shares the neural representation of physical pain (Decety and Chaminade 2003; Eisenberger and Lieberman 2004; Panksepp 2005; Sanfey et al. 2003). Social pleasure shares the neural representation of basic rewards (Immordino-Yang et al. 2009; Izuma et al. 2008; King-Casas et al. 2005; Moll et al. 2006; Tabibnia et al. 2008). Watching others experience physical or emotional pain activates similar brain regions as to experiencing the pain oneself (Morrison et al. 2004; Jackson et al. 2005). Learning from others during social interactions activates the same associative processes as reward-based learning (Behrens et al. 2008).

A universal need to distinguish in- and out-group

Just as would be predicted if it is universal to distinguish in- and out-group, the neural response to observing affective states in others is greater for in-group compared to out-group members (Eres and Molenberghs 2013). The sensorimotor cortex is more activated by the pain of others with whom one shares group membership and emotional closeness (e.g., Beeney et al. 2011; Forgiarini et al. 2011). When explicitly instructed to mimic others' behavior, brain areas underlying imitation are recruited more when the other is from the out-group than from the in-group (Losin et al. 2012). Who is considered in-group and consequently empathic neural responses to pain is of course not fixed (Zuo and Han 2013). Just as would be predicted if having relationship rules is universal, neural evidence shows that people are sensitive to cues implying how to respond to other's pain (Cheng et al. 2007) and whether to trust them (Delgado et al. 2005; King-Casas et al. 2005).

A universal need to innovate

Just as would be predicted if innovation is a universal need, the brain is well equipped to detect and remember novel events and to flexibly adjust behavior on the basis of novel information (Ranganath and Rainer 2003). As would be predicted if the propensity to innovate is for the purpose of facilitating creative solutions to problems the group faces (and allowing in-group mimicking and coopting of innovation), innovation is not the first response. People are sensitive to others' behavior, mimicking until others' responses proven inadequate and only then switching to novel responses (Frith and Frith 2012). Imitation as the source of cultural learning can be traced to neurocognitive mechanisms such as the mirror neuron system (Losin et al. 2009); neural response to faces and objects are influenced by the response of (in-group) others (Campbell-Meiklejohn et al. 2010; Zaki et al. 2011).

Summary

Taken together, neuroscientific evidence supports the idea that cultural universals are both basic and context sensitive. This situational and contextual sensitivity follows from the basic premise that thinking is for doing (James 1890). At a universal level, the brain is equipped to focus on group membership, relational norms and nuances of inclusion and exclusion, social power and prestige, as well as on whether fitting in or sticking out is appropriate. At the particularistic level, these processes are sensitive to which cultural universal is contextually relevant and how things should unfold in a particular society, time, and place.

The proactive brain: predictions and prediction errors

Current neuroscience models suggest a 'predictive' brain facilitates these processes (Brown and Brüne 2012) that continuously and automatically generates (nonconscious) predictions about what is likely to happen and automatically compares these predictions with what actually did happen (for an overview see Bubic et al. 2010). Even the perception of elementary information is rapidly linked to existing mental representations, activating associative networks and representations that most resemble the stimulus (Bar 2007, 2009). The more familiar the stimulus, the more automatic and immediate associations are activated by minimal cues in the environment (Barsalou 2009).

Figure 2 graphically illustrates this prediction process. In brief, the brain responds to (environmental) cues or stimuli, readying for action by generating predictions about each to-be-entered situation based on associative networks.

Associations can be simple and fully automatic, as when we predict the taste of a lemon before eating it. Regions in the medial temporal lobe process these simple (Hebbian) associations (Mayes et al. 2007). A single stimulus can evoke a range of associations, which one is activated depends on immediate context (e.g., a phone can be associated with either work or leisure depending on context). Each activated association activates the next, forming the basis for complex associational networks. Associative network activation can be automatic or deliberate as can be processing of implications to be drawn from activated associations. Associative processing relies on brain areas that are active during unconstrained thought (i.e., the default network), suggesting that associations form the unit of thought. Rather than passively 'waiting' to be activated, the human brain uses these associations to generate testable predictions about future events (Bar 2007, 2009). Prediction generation is often implicit and nonconscious, entailing short-term expectations about current sensational input (Friston 2009). However, prediction generation can also be explicit and conscious and can entail long-term simulations about distinct future events (Bar 2007; Gilbert and Wilson 2007).

Prediction systems rely on continuous feedback about match or mismatch with prediction that is fed back to the predictive system to shift mental effort and allocated attention (e.g., Bar 2009). A match between predictions and the actual situation will result in less error signal at low levels of the neural system (Friston and Stephan 2007). This implies energy saving, indeed, a match between predictions and the actual environment limits attention to the expected, efficiently husbanding brain resources to attend to novelties in the environment (Bar 2009; Schultz and Dickinson 2000).

In contrast, mismatches yield information that the prediction was wrong and allow for learning by attending to the unexpected stimulus and updating the current predictions from lower to higher cortical levels (e.g., Bar 2009; Fletcher and Frith 2008; Friston 2005; Schultz et al. 1997). Updating associative networks slowly improves prediction. Learning from prediction errors takes time because unless the error is clear, an error does not inform what the correct prediction should have been.

Evidence for neuroscientific prediction models

In the last decade a considerable body of neuroscientific research has accumulated, showing the relevance of prediction models for the understanding of complex social cognition, including theory of mind, empathy, imitation, and self- and facial recognition, and decision-making (for overview see Brown and Brüne 2012). Some of these studies demonstrate brain response to predictions about others' intentions. For example a number of studies involve trust games (Behrens et al. 2008; Delgado et al. 2005; King-Casas et al. 2005). In these studies, participants showed increased brain activation reflecting a surprise signal when partner behavior deviated from a tit-for-tat strategy, compared to when partner behavior was according to expectation. This occurred both when the behavior was beneficial or harmful to oneself, with an additional signal in dorsal caudate nucleus distinguishing harmful from beneficial behavior (King-Casas et al. 2005). Moreover, prior positive or negative expectations about partner's behavior reduced this surprise signal and reduced

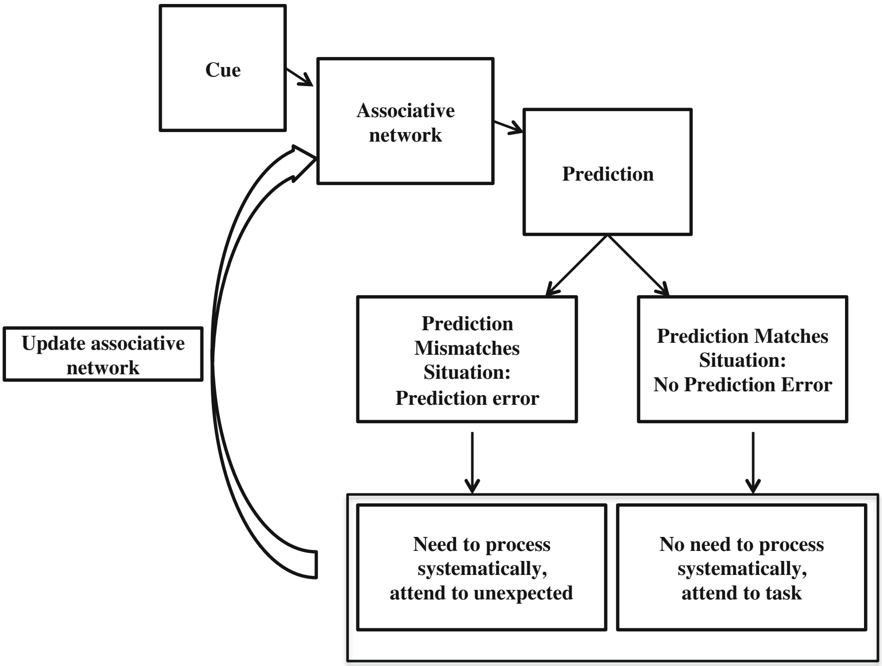

Fig. 2 The neuroscience prediction model. The neuroscience prediction model articulates how the brain updates and by implication, why in spite of high sensitivity to context, acculturation is difficult. Starting at the *top row* from *left* to *right*, an environmental cue activates an associative network, which in turn generates predictions about the situation. If predictions match the situation, no error response is generated. If predictions mismatch the situation, an error response is generated. If there is no noticed prediction error, associative processing focuses on the task. The associative network is updated (to strengthen existing prediction or to add new information). In addition, if there is a noticed prediction error, this yields a shift to systematic processing of the situation to attend to the unexpected. Attending to the unexpected may or may not improve prediction at the next round since why an unexpected situation was encountered cannot be ascertained from registering that an unexpected situation was encountered

behavioral adaptation to partner behavior (Delgado et al. 2005), as would be expected if mismatches go unnoticed in the presence of strong prior predictions. The implication is that once activated, an associative network will influence behavior until sufficient mismatches accumulate to inform network shift. Indeed Roepstorff et al. (2010) argue that from the repetition of (sub)cultural particularized practices (patterned practices) certain predictive models become established in the brain.

Specificity of prediction can require expertise so that in a domain in which one is expert, smaller deviations from prediction will be experienced as a mismatch, allowing experts to finely tune their predictions and their learning process. To study this process, Vuust et al. (2009)examined brain activation of jazz musicians and non-musicians exposed to jazz that included deviations in rhythmic presentation. Brain activity increased more in the jazz than in the non-musicians, suggesting better prediction error detection (i.e., increased mismatch negativity) and subsequent evaluation (increased P3am component) in the jazz musicians who presumably had much more specific predictions and a narrower range of acceptability prior to noticing mismatch to prediction.

Summary

Neuroscience, social neuroscience, and prediction models provide evidence that people are attuned to process information about others and to learn from others and evidence that the brain functions through rapid checks of associative network-based predictions. Predictions ready the brain for the expected. In the case of mismatch between prediction and unfolding reality, attention is allocated to discover the source of mismatch. Higher-level cognitive effort is allocated to mismatch, not to match, to the novel, not the routine. These models set the stage for the use of prediction models in cultural neuropsychology. Integrating these neuroscientific prediction models with the CSC framework yields a set of novel predictions for culture as both a universal and a particularistic process. These predictions are highlighted in the next section.

Integrating CSC and NP models

Integrating CSC and NP models yields the following set of core principles. Thinking is for doing; universal cultural themes make salient group membership, relationships, and innovation as potential targets for action as appropriate in context. The brain prepares for action by making predictions that are generated from associative networks activated by cues in the immediate situation. Given their centrality, cues involving cultural universals (group membership, relationships, managing innovation) should be picked up even if relatively impoverished. Attention should be allocated to mismatch of prediction to particular instantiations of these cultural universals. Within any society, predictions are based in prior knowledge and experience, so matches are more likely if things unfold as expected based on prior experience in a particular culture.

An integration of the CSC and neuroscience prediction model approaches facilitates articulation of the kinds of primes most likely to reliably cue behavioral response. For example, the CSC model implies that a universal element of human culture is group membership, integrating this with prediction models implies that people across societies have dense associative networks about group membership. This integration yields the prediction that priming cultural mindset in a between-group situation should reliably cue collectivist mindset if the out-group boundary is salient and individualism if it is not. Similarly, the CSC model implies that a universal element of human culture is setting up situations in which innovation is supported (so it can be exploited), integrating this with prediction models implies that a core brain function is to learn from others and to innovate only in the absence of relevant others whose responses can be followed. This integration yields the prediction that priming cultural mindset in a novel personal choice or private consumption situation should reliably cue individualistic mindset if there is no social information available but collectivistic mindset if such information is available.

Integrating NP and CSC models also allows for theoretically driven predictions about the neural correlates of cognitive, emotional, and behavioral consequences of universal cultural processes. Specifically, NP models provide insight into likely changes in brain activation depending on whether an individualistic or collectivistic mindset is active during a particular task. That is, an accessible cultural mindset generates predictions as to what will occur. Predictions in turn shape perception of what actually did occur. Only if mismatch is noticed is there a correction signal and switch to systematic processing. If no mismatch is noticed, no prediction error is registered. In these cases, brain activation should be in areas relevant for task execution congruent with the active mindset. On the other hand, if mismatch is noticed, brain activation should switch from task execution to areas associated with prediction-error learning.

As summarized next, current CN research supports some of these predictions and highlights gaps in the current research. In particular, current studies in CN most often provide evidence for the first outcome (match between mindset predictions and task), demonstrated both by EEG (electroencephalogram) and fMRI (magnetic resonance imaging) studies and do not focus on the second (mismatch between mindset predictions and task) (for reviews see e.g., Ambady and Bharucha 2009; Han et al. 2013; Kitayama and Uskul 2011; Rule et al. 2013). This research tradition does not as yet actively consider the interplay between universal and particular cultural processes, yielding gaps for future research.

Current cultural neuroscientific research

Cultural neuroscience starts with the premise that cultural differences should be rooted in distinct brain responses. Though not incompatible with a CSC approach, to date CN research has not typically taken this approach. Instead, research in this tradition typically parses cultural difference in terms of between-society differences in individualism and collectivism, with particular emphasis on documenting neural level differences in participants from individualistic and collectivistic societies using EEG and fMRI techniques. However, if culture involves both universal and particularistic processes, both should be observable in the brain across individuals. This implies that basing the CN research paradigm on cross-national comparison alone is insufficient to understand how the brain is implicated in cultural processes. We searched for CN studies using cultural mindset priming methods by using the keywords (culture or self-construal), (priming or mindset), and (fMRI or EEG or ERP) in the electronic databases Pubmed, Science Direct, and Google Scholar. In this section we review evidence from EEG studies (that document allocation of attention using event-related potential or ERP) and from fMRI studies (that document neural activation of specified brain regions). As will be seen, results support the CSC–NP model. That is, the brain prepares for action by making predictions generated from the associative networks activated by currently accessible cultural mindset. Attention is directed to mindset-congruent stimuli and this is paralleled by increase in brain activation in areas that underlie the mindset-congruent processing.

Evidence from EEG studies

We found four EEG studies in which cultural mindset was primed (Jiang et al. 2013; Lin et al. 2008; Sui et al. 2013; Wang et al. 2013a, b). In one study, Lin et al. (2008) used ERPs to examine neural response to tasks which are congruent versus incongruent with the mental procedures that a cultural mindset brings to mind. They started with prior behavioral research with European American (Kühnen and Oyserman 2002) and Chinese (Lin and Han 2009) participants demonstrating that salient collectivistic rather than individualistic mindset improves speed of detection of big letters made up of little letters, with the reverse pattern found for speed of detection of the little letters themselves. Attention to little letters is increased when an individualistic mindset is accessible and attention to big letters is increased when a collectivistic mindset is accessible. Lin et al. (2008) used the same priming method these other studies had used, they asked participants to note first person plural or first person singular pronouns in paragraphs. As before, participants were then presented a big letter made up of smaller letters and asked to identify either the big or little letter. Lin et al. (2008) showed that individualistic-mindset resulted in larger P1 amplitude (occipital electrodes peaking at 90 ms) in the extrastriate (visual) cortex at lateral occipital electrodes when responding to the little compared to the big letters. In contrast, collectivistic-mindset resulted in larger amplitudes when responding to the big than the little letters. Mean P1 amplitude to the big and little letters in the control condition did not differ. From an NP perspective, this implies that the activated cultural mindset increases attention to mindset-congruent stimuli at an early stage of visual information processing.

In a second study using cultural mindset priming and ERP, Sui et al. (2013) show that priming a cultural mindset influenced attention only if the mindset was *not* the one likely to be chronically accessible. In this study, British and Chinese participants were asked to identify the orientation of their own and friend's faces (left or right). Control condition and collectivistic-mindset condition Chinese participants showed an anterior N2 neural response to friend's face orientation that decreased in the individualistic-mindset condition. Control condition and individualistic-mindset condition British participants showed an N2 neural response to own face orientation that decreased in the collectivistic-mindset condition. From an NP perspective, the N2 response suggests salience. With this interpretive lens, the results imply that under the assumed chronic mindset (collectivism for Chinese, individualism for British), seeing a friend is salient for Chinese participants and seeing oneself is salient for British participants. If an individualistic mindset is primed, friend's face becomes less salient for Chinese participants. If a collectivistic mindset is primed, own face becomes less salient for British participants.

The last two EEG studies focused on the effects of cultural priming on pain perception. Wang et al. (2013a) induced physical pain in Chinese participants' left hands after priming them with either individualistic or collectivistic cultural mindsets. They found that priming individualistic cultural mindset increased early somatosensory activity (larger N130 amplitudes) in the frontal/central regions in response to physical pain (0.5 ms electrical stimulations). This study suggests that an individualist mindset increases self-focus thereby enhancing the neural response to stimuli applied to the self. Jiang et al. (2013) presented Western and Chinese participants with pictures showing a strangers' hand experiencing pain or no pain after priming them with either individualistic or collectivistic cultural mindset. Participants were asked to judge whether the unknown target felt pain. ERP amplitude recordings demonstrated that early automatic empathic neural responses (fronto-central activity at 232–332 ms) decreased for Western participants primed with individualistic mindset and for Chinese participants primed with collectivistic mindset. This study suggests that a cultural mindset prime that is congruent with one's (assumed) chronic cultural mindset decreases pain perception in the brain. It is not quite clear how these results should be understood. Literature on individualism and collectivism would not predict such a result since effects are not due to individualism or collectivism and people show less pain response when the presumed dominant mindset is primed. Jiang and colleagues suggest the following interpretation, which is that priming collectivistic mindset highlights the salience of in-group out-group boundaries for Chinese, while priming individualistic mindset highlight the salience of boundaries between self and others for Americans. It is not clear why the prime works differently between samples and this may be an artifact of how the samples were obtained. That is, the Western participants were undergraduate or graduate students who had been in China less than a month and given their outsider status, may have been chronically primed to consider themselves as different from all others.

Evidence from fMRI studies

We found six fMRI studies in which cultural mindset was primed, most of these focused on neural mechanisms underlying self- and other-representation (Chiao et al. 2010; Harada et al. 2010; Ng et al. 2010; Sui and Han 2007). These studies focus on a set of regions, the right middle frontal cortex, the ventromedial prefrontal cortex (vMPFC), and the posterior cingulate cortex (PCC), that are part of the default network—regions that are active in rest. This activity is interpreted as self-focused processing (Moran et al. 2013). Performing tasks not related to self-processing leads to suppression of this activity (although there is discussion about the question of which task characteristics actually decrease activity compared to rest). In the six studies we found the tasks of interest involved self-processing and so, to a greater or lesser degree, invoke processes similar to rest. These regions are the focus of attention given the assumption that a core element of the distinction between individualism and collectivism involves whether the self excludes others (highlighting unique attributes of the self, emphasizing difference between self and others) or includes others (highlighting relationships and group memberships, emphasizing similarity between self and others). As detailed next, these studies demonstrate larger differential activation of these brain regions when processing self and other-relevant information (about close others as well as about out-group members) when an individualistic mindset rather than a collectivistic mindset is accessible.

Two studies (Ng et al. 2010; Sui and Han 2007) showed differential brain activation during processing of self-relevant information if individualistic rather than collectivistic mindset was primed. For example, Ng et al. (2010) showed participants adjectives and asked them whether they described themselves (self-judgment), their mother (mother-judgment), or a person they do not identify with, excluding their parents (other-judgment). Primed individualistic mindset yielded differentiated vMPFC activity between self and other judgments and between self and mother judgments, primed collectivistic mindset did not.

A third study used a similar paradigm but an implicit task (Harada et al. 2010). Harada and colleagues asked participants if a word phrase relevant to themselves, their father, or an unfamiliar person appeared on the right or left side of the screen. Participants primed with individualistic mindset showed greater activation due to less deactivation in the dMPFC during evaluation of father-relevant as compared to self-relevant information. When primed with collectivistic mindset, dMPFC activation did not differentiate as a function of person (self, father, stranger).

A fourth fMRI study primed cultural mindsets and asked participants to make general or context-specific self-judgments—e.g., "In general I am humble", or "When I am with my mother I am humble" (Chiao et al. 2010). Participants in the individualistic mindset condition showed increased activation in the vMPFC and PCC regions for general rather than contextual self-judgments, participants in the collectivistic mindset condition showed increased activation in these same regions for contextual rather than general self-judgments. In both cases, activation implies that the task is congruent with self-processing.

A fifth fMRI study (Varnum et al. 2014) focused on the effect of cultural mindset priming on reward processing. Chinese participants were involved in a card game in which they had to guess whether a card had a number higher or lower than 5. Correct guesses resulted in monetary rewards, incorrect ones in losses. In some trials the gains or losses were for themselves, in other trials the gains and losses accrued to a friend. Priming condition significantly affected activation in "reward regions" (ventral striatum) in response to winning money: reward activation for oneself and one's friend was similar in collectivistic-primed participants, whereas reward activation for oneself was greater than for one's friend in individualistic-primed participants. Furthermore, collectivistic-primed participants showed greater activation in an "empathy region" (right insula) in response to losses for one's friend compared to losing oneself, whereas this pattern was reversed in individualistic-primed participants.

A final fMRI study focused on the effect of cultural mindset priming on readiness to act prior to rather than during a task (Wang et al. 2013b). This study took advantage of the fact that neuroimaging allows for examining the neural correlates *during* cultural priming as well as during resting state after priming and before task instructions. Among the Chinese participants in this study, compared to control and collectivistic mindset conditions, priming individualistic mindset decreased activation in brain areas that are known to be involved in other person perception and inference of others' mental states, including the dMPFC and left middle frontal cortex. The authors also examined brain activation after the priming task, during resting state. Results revealed increased regional homogeneity (i.e. similarity of dynamic fluctuations of voxels) in the dMPFC, but decreased regional homogeneity in the PCC in the collectivistic mindset and control conditions compared to the individualistic mindset condition. These results are congruent with our integration of CSC and prediction models, such that salient cultural mindset triggers an associate network in preparation for incoming stimuli even in a "resting state".

Summary

Current CN fMRI research utilizing cultural priming techniques primarily focuses on activation of neural regions associated with self in response to processing descriptors relevant to self versus others or to processing information about self versus others more generally. It should be kept in mind that interpretation of fMRI studies uses what has been called 'reverse inference', by which the engagement of particular cognitive functions is based on activation in particular brain regions (Poldrack 2006). The strength of inference that can be drawn from this reasoning strategy is dependent on the degree to which this region is selectively associated with the cognitive process of interest. With that caveat, the results of these studies lend support to parts of the CSC model as illustrated in Fig. 1. First, the study by Wang et al. (2013b) shows that subtle environmental cues (e.g., reading a story with singular or plural pronouns) can activate relevant cultural mindsets and their associative networks as seen in the activation of particular regions in the brain during a priming task or during resting state. Individualistic cues decrease and collectivistic cues increase activation in brain regions involved in processing other-relevant information. Second, the studies by Ng et al. (2010), Sui and Han (2007), and Harada et al. (2010 show greater differential activation when processing of self-relevant compared to other-relevant stimuli among individualistic mindset primed participants, whereas activation in this same region did not differentiate between self- and other-relevant stimuli among collectivistic mindset primed participants, implying that associative networks relevant to both individualistic and collectivistic mindsets are being cued. Third, across studies findings imply that accessible cultural mindset cues an associative network that yields a particular process, goal or content domain salient. This process, goal or content domain then influences behavior. Because effects are often indirect, via spreading activation, effects are probabilistic rather than certain.

Whereas the behavioral evidence shows that both cultural mindsets can be primed, with control condition responses falling somewhere between individualistic and collectivistic mindset condition responses (Oyserman and Lee 2008), the results from the EEG studies are less clear. A number of studies show activation difference for participants assigned to in the mindset condition less likely to be chronically activated or activation differences not easily linked to a simple individualism vs. collectivism dichotomy. The results of the studies by Lin et al. (2008) and Wang et al. (2013a) are congruent with the notion that the activated mindset focuses attention on a mindset congruent stimulus. However, two other studies found differential results depending on whether the activated mindset was congruent with the dominant mindset. In the study by Sui et al. (2013) effects on attention were only found for participants assigned to the mindset condition less likely to be chronically activated. In contrast, activated mindset influenced empathy for pain only when it was compatible with the chronic mindset in the study by Jiang et al. (2013).

From the NP perspective it would seem that cueing the dominant cultural mindset would be more effective because it does not require any switching. However, that does not help in explaining these results, because the results of the two studies are opposing. Given the unexpected findings from these studies, followup research is needed to more systematically elucidate effects of priming mindset congruent or incongruent with dominant mindset. Studies have also not yet attended to when predictions do not match the task. Taken together, results of CN priming studies support the notion that the brain prepares the individual by making predictions and that brain activation increases after perception of mindset-congruent stimuli. To date CN research has proceeded narrowly without consideration of cultural universals or the particularistic elements of culture. As outlined next, an integration of CSC and the NP models yields a number of novel research questions and hypotheses to be addressed in future cultural neuroscientific research.

Gaps and future directions for cultural neuroscience research

To date, CN researchers have focused on demonstrations of differing patterns of neural response between people assigned to individualistic and collectivistic mindset conditions. With a few exceptions, CN has not yet tested CSC predictions about the universal and particularistic nature of cultural processes. Emerging research examining the effects of cultural mindset priming on sensitivity to pain of in- and out-group others (Wang et al. 2013a) and on neural activation (readiness to act and make meaning) prior to a task being presented (Wang et al. 2013b) are promising first steps.

Research to date has not tested consequences for neural response of cuing each of the universal cultural elements: group membership, fitting into relationships, and support for innovation. Moreover, research to date has not provided a theoretical articulation of which particular priming tasks should be robust activators of individualistic and collectivistic mindsets across societies. Following CSC, it should be the case that cues closely related to innovation, group memberships, or interpersonal relations should universally prime individualist and collectivistic mindset. Whether a particular priming task works across societies should depend on how closely associated the task is to these universal elements. A straightforward next step would be to test the neural consequences of these primes during a resting state after priming.

Current CN studies already provide some support for the universality of individualistic and collectivistic mindsets by showing similar brain activation during a task after priming individualistic and collectivistic mindsets across cultural groups. The research paradigms of most of these studies are set up in a way that the predictions generated from the accessible cultural mindset are needed for task requirements (e.g., judging self and other-relevant information). This means that activation occurs in relevant brain areas congruent with the active mindset. Missing from current research is examination of neural response if prediction does not match stimuli. Behaviorally, this has been examined as cultural disfluency (Oyserman 2011; Mourey et al. 2014). An activated cultural mindset should organize prediction and focus attention, yielding higher level neural activity if prediction is met and lower level updating if prediction is not met.

Because CN studies have not been set up to test either response to whether predictions are met or the downstream consequences of match or mismatch to prediction, a number of important questions have as yet been unaddressed. First, what evidence is needed for a mismatch to be noticed? Second, does the nature of the needed evidence change if the cued cultural mindset is generally the dominant one? Third, what is the process from noticing a mismatch to getting a correct prediction—and is this process symmetric, equally lengthy and difficult if starting from an individualistic or a collectivistic frame?

The answers to these questions would be useful in understanding the persistence of errors, difficulty in acculturation, and other socially and politically important considerations relevant to culture and cultural diversity. On the one hand, people should be able to relatively easily switch between individualistic and collectivistic mindsets. On the other hand it is not clear how or when they would notice that predictions based in one cultural mindset do not match the situation.

At the same time, formulating culture in terms of cultural particulars would highlight the need to study consequences for neural response of cuing elements that are particular to one society and not another. Cultural particulars are part of the tacit knowledge included in associative networks in a specific society, time, and place. Cultural expertise in a particular society implies that one has detailed knowledge of how situations will unfold; this expertise means that even small shifts from expectation are detected and require processing. Neural prediction research has shown this for example by studying neural response to hearing improvisations among jazz experts and novices (Vuust et al. 2009). Cultural as situated cognition research has demonstrated that people reason and act differently in contexts that unfold as culturally expected compared to contexts that unfold not quite as expected (Mourey et al. 2014). For example, Hong Kong Chinese but not American participants choose larger portions when given red-bordered plates rather than black-bordered plates during Chinese New Year, the month after Chinese New Year, plate border color no longer matters (Mourey et al. 2014). Follow-up studies demonstrating effects at the neural level will allow for a test of the CSC–NP integration.

In addition to its usefulness for study of both universal and particularistic aspects of culture, an integration of CSC and NP models allows for more nuanced study of acculturation. In particular a CSC–NP model yields insight into core questions of why it is so difficult and often remains incomplete after many years and much effort. CSC studies to date make clear that what constitutes particular cultural knowledge remains hidden and unnoticed if predictions match situation as it unfolds, focus is on the task and not on the prediction, until one visits or immigrates to another country. Following NP models, successful acculturation requires attention to be focused on whether predictions are matched. Yet whether a prediction matches an unfolding situation is likely to be unclear outside of one's own society, apparent matches may be misinterpretations and even if a mismatch is noticed, correction requires knowing what the underlying prediction should be which is different from simply noticing an error in prediction. Integrating CSC and NP models implies that mismatches often go unnoticed and noticed mismatches may never yield accurate insight as to the process. An immigrant may simply notice 'they do not do what I expect' without knowing what 'they' are doing or what 'they' think what they are doing means.

In order to function successfully and integrate in a new society, sensitivity to cultural universals is insufficient. To generate accurate predictions and act appropriately in everyday life one must learn the particular ways these universals are instantiated, the specific details of how things are done in one's new society. NP models would predict that acculturation processes are not quick and easy, but rather lengthy and difficult. Mismatches between one's predictions and the new situation are often not detected and when they are, the nature of the error is at first unlikely to be clear. This does not mean that culture-particularized practices can never be understood by an outsider, but rather that the process is likely to be long and unlikely to be complete because it involves trial and error rather than rule-based application of a general principle. In addition, it is likely that correct feedback is crucial to notice that current predictions were wrong and that these need to be adjusted. It is likely that people differ in their ability to be sensitive to this feedback, and at the same time context differs in the likelihood that feedback will be clear or sensitively provided. Consequently, it might be that some people never understand the details of the new society and that some societies are more difficult to learn from the outside in. An integration of CSC and neuroscience prediction models highlights why that might be and also suggests interventions that might help address these difficulties of acculturation.

By rethinking the mind–brain–culture–behavior interface, our goal is to highlight both gaps in current research and useful applications of research to everyday situations people face. From a theoretical perspective, integrating CSC and neuroscientific prediction models highlights both that cultural universals should be prime-able across societies and that the particular contextual cues that evoke them may be substantially different across societies. Our integration also highlights why it is that priming cultural universals results in probabilistic but not deterministic effects, since how the associative network is entered and the specifics of the situation matter for the strength of the prime and its closest associates. Finally our integration highlights why engaging in a culture feels natural unless the culture is a new one, and then it is experienced as effortful and taxing.

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