

CONTEXT EFFECTS ON THE NEURAL CORRELATES OF EMOTION

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ABSTRACT

Joseph Leshin: Context Effects on the Neural Correlates of Emotion
(Under the direction of Kristen Lindquist)

Human emotions are inextricably linked to the context in which they occur, yet neuroscience research on emotion often overlooks the role of context in shaping the neural correlates of human emotions. This dissertation, through three studies, begins to address this gap. Study 1 (Chapter 2) investigated how language as a form of context influences the brain's response to facial expressions of anger and disgust, showing distinct differences in neural activity related to disgust perception between Chinese Asian and White American participants. Language was found to play a significant role in shaping the neural correlates of emotion perception, particularly in the context of disgust for Chinese Asian participants. Study 2 (Chapter 3) examined the influence of social and cultural contexts on the neural correlates of fear and sadness, demonstrating that both cultural group membership and cultural attitudes are related to the brain's processing of negative emotional experiences. Study 3 (Chapter 4) focused on individual and group level variation in emotion-related functional connectivity, finding both idiographic and nomothetic patterns of connectivity related to negative emotional experiences. It further highlighted the influence of cultural attitudes on the neural correlates of emotion. Overall, these studies illustrate the importance of considering diverse contextual variables in studying the neural basis of emotion. They show that social and cultural contexts influence how the human brain processes and represents emotions.

Pura fe en el morir, pobre alegría
y macabro danzar antes de tiempo.

—Antonio Machado

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CHAPTER 1: CONTEXT EFFECTS ON EMOTION

Introduction

Human emotions are inextricably linked to the contexts in which they occur (Aldao, 2013; Barrett et al., 2011; De France & Hollenstein, 2022; Gonzalez-Liencres et al., 2013; Greenaway et al., 2018; Immordino-Yang, 2010; Koban et al., 2021; Kring & Campellone, 2012; Maren et al., 2013; Martinez, 2019; Mesquita et al., 2017; Power & Dalgleish, 2015; Scarantino et al., 2021; Scheer, 2012; Scherer & Moors, 2019; Szekely et al., 2017; Telzer, 2010; Todd et al., 2020; Uchida et al., 2022; Verduyn et al., 2015). Here *context* refers to the available information surrounding an event (Barker & Warburton, 2020; Robertson et al., 2015), and most emotion theories would agree that the context in which emotional events occur will in part predict which emotion a person will feel (Boiger et al., 2018; Brose et al., 2013; Coifman et al., 2016; Hess et al., 2020; Kitayama et al., 2006; Locke et al., 2015; Power & Dalgleish, 2015; Quiñones-Camacho & Davis, 2020; Zelenski & Larsen, 2000) or how that emotion will unfold (Adam & Brett, 2015; Atias et al., 2019; Comtesse & Stemmler, 2016; Fröber & Thomaschke, 2021; Gerger et al., 2014; Ito et al., 2013; Kret & de Gelder, 2010; Mondloch, 2012; Mummenthaler & Sander, 2012; Namba et al., 2020; Pochedly et al., 2012; Yildirim-Celik et al., 2022). Yet despite clear evidence in affective science for context effects on emotion (Greenaway et al., 2018), evidence for these effects in affective neuroscience remains scarce (see Barrett & Satpute, 2019; Lieberman, 2012; Panksepp et al., 2017). Such investigations may be scarce because until recently, the prevailing theoretical framework in affective neuroscience assumed that emotions are instantiated by specific neural substrates in a consistent manner across individuals and situations. This theoretical assumption has limited our understanding of the role of context in the neural substrates of human emotions (for discussions, see Huang et al., 2018; Lindquist et al., 2012; Wager et al., 2015; Xu et al., 2021; Zheng et al., 2022). This dissertation begins to address this gap.

Investigating context effects on the neural basis of emotions may lead to a deeper understanding of the correspondence between neural activity and cognitive function during emotion. The ability to model

context effects on the neural basis of emotions may, for example, help to optimize brain-computer interface tools that seek to infer a person's mental state from their brain activity (e.g., see Du et al., 2019; Kriegeskorte & Diedrichsen, 2019). Moreover, modeling contextual variation may not only facilitate the growing efforts to create context-sensitive emotion-recognition software (e.g., C. Chen et al., 2016; Kosti et al., 2017; J. Lee et al., 2019), but also promote clinical efforts to map contextual factors, such as cultural factors, to neural processes underlying emotion-related psychopathology (Aldao, 2013; Bylsma et al., 2011; De Vaus et al., 2018; Kirmayer et al., 2017; Qu et al., 2021). But perhaps most importantly, an explicit consideration of context effects on the neural basis of emotion may lead to a greater appreciation of human variation (see Arnett, 2008; Blasi et al., 2022; Dotson & Duarte, 2020; Heft, 2013; Lindquist et al., 2022; Qu et al., 2021) that would be well suited to address issues of replicability in human-subject research (Gelman, 2015; Van Bavel et al., 2016; see also Barrett, 2022; Barsalou et al., 2010; Siegel et al., 2018). The purpose of the present dissertation is to begin empirically manipulating and assessing the role of context on the neural basis of emotion; to do so, the following three studies proposed by this dissertation draw on constructionist theories of emotion (e.g., Barrett, 2022; Lebois et al., 2020; Satpute & Lindquist, 2019; Wilson-Mendenhall et al., 2019) that hypothesize that the brain relies on the ongoing context and knowledge about prior experiences to represent—and thus respond to—current emotional events.

Constructionist Theories of Emotion

Theories are much more than sets of explanations for how emotions operate—they are philosophical lenses through which observations are made, hypotheses are generated, studies are designed, and data are interpreted (Kuhn, 1977). Constructionist theories of emotion have long held that discrete emotion categories like “fear” and “sadness” lack consistent and unique behavioral action tendencies (Baumeister et al., 2007; DeWall et al., 2016; Durán & Fernández-Dols, 2021), facial behaviors (Jack et al., 2012, 2016), peripheral physiological signatures (Siegel et al., 2018), or unique and specific causal mechanisms in the brain (Guillory & Bujarski, 2014; Lindquist et al., 2012; Wager et al., 2015). These theories recognize that heterogeneity in the behavioral actions, facial behaviors, physiological reactivity, and brain activity associated with an emotion category such as “fear” is the norm, not the exception (Hoemann et al., 2020; Lindquist et al., 2022). For instance, although traditional

theories of emotion (e.g., see Ekman & Cordaro, 2011; Panksepp & Watt, 2011) assume that an emotion category like fear names a set of instances that share a key set of features with a common causal mechanism, some instances of fear feel good and some feel bad (Wilson-Mendenhall et al., 2013a), some involve an increase in heart rate and some involve a decrease (Kreibig, 2010), and some involve significant activation within the amygdala and some do not (Kober et al., 2008; Lindquist et al., 2012). The notion that there are central organizing mechanisms that produce an emotion such as fear (e.g., a dedicated fear nucleus, circuit, or single brain activation pattern) are now highly debated in affective neuroscience (Barrett & Satpute, 2013; LeDoux, 2014; Lindquist et al., 2012; Touroutoglou et al., 2015). The current dissertation thus proposes that a factor contributing to the heterogeneity in the neural basis of emotions (e.g., see Huang et al., 2018; Lindquist et al., 2012; Qi et al., 2018; Wager et al., 2015; Xu et al., 2021; Zheng et al., 2022) is the context in which emotions occur.

According to constructionist theories of emotion, emotions are “situated conceptualizations” that occur when a brain uses prior experiences stored in memory to make meaning of sensations inside the body (interoception) and outside the body (e.g., visual, auditory, olfactory, etc. sensations) as an instance of an emotion such as “fear” or “anger” (Barrett, 2017; Wilson-Mendenhall et al., 2011). The availability and accessibility of emotion concept knowledge influences this process as emotion concepts are thought to be mental representations of situated actions and feelings that were adaptive in similar contexts in the past (Barrett, 2017; Lindquist, 2013; Satpute & Lindquist, 2019). Thus an emotion concept, such as “anger,” represents a set of highly variable, situated instances—for example, anger during a fight with a spouse or anger at a slight by a boss or anger when the cat pees on the bed—that are grounded by modality-specific information tied to the situations in which they occur (Kreibig, 2010; Siegel et al. 2018; see Barrett, 2017). Furthermore, according to constructionist models of emotion, emotion concept knowledge is supported via domain-general processes such as abstraction, categorization, and socialized, culture-specific emotion categories learned through language (Barrett, 2017; Lindquist et al., 2022; Satpute & Lindquist, 2019). Our theoretical framework proposes that emotion category words or concepts such as “anger” help to cohere together otherwise highly variable situated instances as members of the same category (Atzil & Gendron, 2017; Doyle & Lindquist, 2018; Hoemann et al., 2019; Wilson-Mendenhall et al., 2011). Such words serve as “essence placeholders” (Medin & Ortony, 1989)

that allow individuals to see highly variable instances as similar in terms of a shared abstract meaning or goal (Lindquist, 2013; [Lindquist et al. 2022](#); Satpute & Lindquist, 2019).

Constructionist theories of emotion thus offer specific testable hypotheses for the impact of context on emotions. First, unlike theories that propose the existence of neurons that are genetically encoded to produce specific emotion categories and consider context as separate from the processes that create emotions (Tracy & Randles, 2011, p. 398; see also Celeghin et al., 2017), a constructionist perspective on emotions views contextual factors as playing a constitutive role in shaping the neural basis of emotions. Specifically, if emotions are “situated conceptualizations” (Barrett, 2017; Wilson-Mendenhall et al. 2011), then emotions should be inextricably bound to the situation in which they occur. That is, fear of an intruder should be instantiated by different neural mechanisms than fear of heights insofar as those instances have different situational affordances, behaviors, and subjective feelings.

Second, and relatedly, constructionist theories of emotion advocate for empirical investigations in the potential for dissimilar neural representations to support the same emotion category (Barrett & Satpute, 2019). The idea that multiple mechanisms can achieve the same result is demonstrated in complex systems, including biological systems that adapt to their environments (Edelman & Gally, 2001; Marder & Taylor, 2011; Sporns et al., 2000; Tononi et al., 1999; Whitacre & Bender, 2010). Thus, a constructionist perspective on emotions hypothesizes that there is diversity in the neural mechanisms for an emotion category such as fear that reflect the situational variation and context-specific demands of said fearful experiences (Doyle et al., 2022). The lack of success in finding brain biomarkers for specific emotions that transcend contexts (e.g., see Xu et al., 2021) supports this constructionist viewpoint that the diversity among instances of an emotion category is a real and meaningful phenomenon imposed, in part, by the context in which those instances occur (Barrett, 2022; Barrett & Satpute, 2019; Clark-Polner et al., 2016; Doyle et al., 2022).

Third, some constructionist theories emphasize that words serve as cues to concept knowledge of emotion and therefore facilitate situated conceptualizations of emotion. Accessing concept knowledge relies on language because language enables the acquisition of abstract concept knowledge during learning and retrieval of semantic knowledge through the use of descriptive terms such as “excited” or “anxious” (Cunningham & Kirkland, 2012; Lindquist, 2013; Satpute & Lindquist, 2021). Indeed, language

is thought to help construct emotional experiences and perceptions by helping to guide predictions about the meaning of ambiguous affective states, whether those affective states are from one's own internal body during emotion experience or one's external world during emotion perception (Brooks et al., 2017).

Critically, constructionist theories focus on the role of context in both emotional experiences—defined as experiencing a feeling in one's own body or “having” an experience of a particular emotion category—and emotion perceptions—defined as perceiving an instance of an emotion category in someone else’s facial, vocal, or bodily behavior (see Lindquist, Satpute, et al., 2015 for a discussion). A constructionist approach to emotions posits that emotional experiences and perceptions are interlinked as the brain uses semantic knowledge to refine sensory data, whether from the internal body in the context of emotion experience or the external world in the context of emotion perception, into specific emotions such as excitement, anxiety, and so forth, that are relevant to the immediate context.

Evidence for the Role of Contextual Factors in Emotion

Behavioral evidence for context effects on emotion experience and perception is abundant. Historically, research in affective science has focused on person and situational factors as the forms of context most likely to influence emotional events (Aldao, 2013; Barrett et al., 2011; Bartz et al., 2011; Greenaway et al., 2018; Kring & Campellone, 2012; Mesquita & Boiger, 2014; Scherer et al., 2011). Person-level context encompasses processes that operate within the mind of a person, such as gender identity, prior experiences, and linguistic and cultural factors that have been found to impact emotion expression, perception, and experience at the individual level (Barrett et al., 2011; Chiao, 2015; Crafa & Nagel, 2020; Firat, 2021; Gendron et al., 2020; Kring & Campellone, 2012; Lindquist et al., 2022; Uchida et al., 2020). In contrast, situational context can be defined as the basic perceptual features that coincide with an emotional event, such as the presence of depicted, imagined, or actual human others (Arioli, Basso, et al., 2021; Barrett & Kensinger, 2010; Cao et al., 2014; Deng et al., 2022; Hess et al., 2020; Kret & de Gelder, 2010; Phan et al., 2004; Vieira et al., 2020; Vrtička et al., 2011).

Whereas ample behavioral evidence demonstrates the role of linguistic, cultural, and situational context on emotion, much less has investigated the role of these forms of context in shaping the neural representation of emotions. Herein, I review the evidence for each form of context on behavioral

outcomes and discuss any existing evidence for such context effects on the neural representation of emotion. These findings set the stage for the integrative dissertation studies.

Cultural and Linguistic Effects on Emotion

Contextual influences on emotion include those operating within the mind of the individual who is experiencing or perceiving the emotion. These contextual influences include cultural norms and culture-specific knowledge, including emotion knowledge.

Culture, more specifically, is both a personal and social concept, although much of the extant theory and research on culture emphasize its social, collective nature in which culture is created, shared, and updated by groups of people, such as institutions and societies (see Denkhaus & Bös, 2012; Han & Ma, 2014; Overton & Müller, 2012; Shkurko, 2020). Yet, simultaneously, culture is internalized and shaped by the individual (e.g., see Collardeau et al., 2022; Crocetti et al., 2022; Nasie et al., 2016; Rizzo et al., 2022; Telzer et al., 2016), creating a cycle of mutual construction between the personal and the social dimensions of culture (Causadias, 2020; Crafa & Nagel, 2020; Markus & Kitayama, 2010; Mesquita et al., 2017; Overton & Müller, 2012). It is for this reason that the present dissertation adopts this person-social dimension of culture to recognize the interconnectedness of the personal and the social in constructing cultural phenomena.

Critically, the transmission of culture-specific emotion knowledge from person to person—and from generation to generation—depends on human language (see Lindquist et al., 2022; Silverstein, 2004). The language one speaks or signs can influence ostensibly nonlinguistic cognitive domains (Blasi et al., 2022), including memory (Q. Wang, 2021), perception (Boroditsky, 2001; Boudelaa & Marslen-Wilson, 2015), decision-making (Costa et al., 2017; Miozzo et al., 2020), social cognition (Kinzler, 2021; Orvell et al., 2017; Packard & Berger, 2020), and, of course, emotion (Brooks et al., 2017; Pavlenko, 2017; Satpute & Lindquist, 2021). Additionally, there is evidence that different languages represent emotion concepts differently (e.g., Jackson, Watts, et al., 2019).

Culture consists of the shared beliefs, values, customs, behaviors, and artifacts that characterize a group or society and that ultimately shapes the way persons think, feel, and behave (Causadias et al., 2018b, 2018a). Culture is a form of context insofar as it provides a framework for understanding and interpreting the world (Scheer, 2012). Although culture can be operationalized in several ways, it has

often been operationalized as race (e.g., Asian, White), nationality (e.g., Chinese, US American), cultural norms (e.g., collectivist, individualist), or a combination thereof in both psychology and neuroscience (for a discussion, see Denkhaus & Bös).

Culture can serve as a context for emotion in several ways. First, culture has been shown to have a significant effect on the way individuals experience and express emotions (e.g., Greenaway et al., 2018; Uchida & Oishi, 2016). Different cultures may have different norms and expectations for how emotions should be displayed and expressed, resulting in distinct modes of experience and expression across societies (Eid & Diener, 2001; Liu et al., 2018; Matsumoto, Yoo, et al., 2008). Some cultures, for example, may place a higher value on the expression of positive emotions and discourage the expression of negative emotions (e.g., Koopmann-Holm & Tsai, 2014; Miyamoto et al., 2014), while other cultures may place a higher value on emotional expressiveness in general (e.g., see Deng et al., 2019). Culture can also shape the way individuals interpret and make sense of emotions. Different cultures may have different interpretations and meanings attached to certain emotion categories (e.g., see Jackson et al., 2019; Mesquita et al., 2017), and these interpretations can influence how culturally-informed individuals experience and understand their own emotions (Zhou et al., 2021). For example, some cultures may view sadness as a sign of weakness, while others may view it as a natural and acceptable response to difficult situations (see Bastian et al., 2012, 2017).

Notably, cultural differences in emotion can be observed at the neural level (see Han & Ma, 2014 and Shkurko, 2020 for reviews). For example, a meta-analysis of cultural neuroscience studies on emotion perception involving East Asian and (predominantly) White Western participants found that East Asian participants, relative to White Western participants, showed greater activation in the dorsomedial prefrontal cortex (DMPFC) when consider the mental states of others (Han & Ma, 2014). This finding is intriguing given that the DMPFC is consistently activated during the perception of social stimuli (Van Overwalle, 2009) and the consideration of others' psychological states (Lieberman et al., 2019). It is also interesting insofar as East Asian participants, more than White Western participants, show heightened context-sensitivity characterized by prioritizing the mental states of others over the self (e.g., Korn et al., 2014; Sui et al., 2013). Other work in cultural neuroscience has shown differences in amygdala activation between cultural groups during emotion perception, typically illustrating that amygdala activity is greatest

when perceiving the emotions of in-group versus out-group members (e.g., Chiao et al., 2008; Harada et al., 2020; but see Derntl et al., 2009; Moriguchi et al., 2005). Of note, very little cultural neuroscience research has examined the neural basis of emotional experiences, although some studies have examined empathy (Han & Ma, 2014) or regulation of emotional experiences (Qu & Telzer, 2017) cross-culturally and found neural differences related to culture.

Altogether, prior work strongly suggests that culture plays a significant role in shaping the neural basis of emotions. Yet the notion that culture has an effect on the brain basis of emotions because of its contextual attributes is often an implicit one; rarely, if at all, is culture explicitly acknowledged as context in the neuroscience of emotion, particularly in research whose samples are predominantly White North Americans or Europeans (e.g., see Denkhaus & Bös, 2012; Dotson & Duarte, 2020; Martínez Mateo et al., 2012; Qu et al., 2021 for discussions). The present dissertation addresses this issue.

Culture may also have an impact on emotion because it shapes the nature and structure of emotion concept knowledge. Adults, for example, show structured conceptual representations of emotions (Barrett, 2017; Barsalou et al., 2010; Wilson-Mendenhall et al., 2016) that help them understand and regulate everyday affective experiences (see Atzil et al., 2018; Atzil & Gendron, 2017; Granat et al., 2017). Further, ample evidence suggests that such emotion concepts influence how a person behaves in an emotional situation (K. M. Lee et al., 2018; Lindquist & Barrett, 2008; see Lindquist, Satpute, et al., 2015 for a review) and what they perceive on the faces of others (e.g., Jack et al., 2016; see Lindquist & Gendron, 2013 for a review). Emotion concepts therefore play a critical role in making predictions about emotional events and choosing appropriate actions to manage them (Cunningham & Kirkland, 2012; Hoemann et al., 2021; K. M. Lee et al., 2018; Lindquist & Barrett, 2008). Critically, concept knowledge about emotion differs as a product of a person's cultural upbringing (Mesquita et al., 2017; Markus & Kitayama, 2010) because terms and concepts used to describe emotional states vary by cultural contexts (Jackson, Watts, et al., 2019; Zhou et al., 2021; see also Veissière et al., 2020). Emotion concepts are acquired throughout human development (e.g., see Gopnik & Wellman, 2012), in which infants and children learn the emotion concepts for regulating physiological imbalances or reactivity, navigating emotional situations, and perceiving emotions in others via socialization from their caregivers (Atzil & Gendron, 2017; Hoemann et al., 2019; Locke et al., 2015; Shablack & Lindquist, 2019; Tan et al., 2020;

Widen, 2013). As a result, the development of emotion concepts is situated within a culture's knowledge and norms about emotion concepts (Chiao, 2018; E. L. Davis et al., 2020; Gendron et al., 2020; Harris et al., 2005; X. Li et al., 2022; Pavlenko, 2004). That is, caregivers instill in children the emotional content, including beliefs, expressions, and regulation strategies, pertinent to their culture's social ecology and expectations (De Leersnyder et al., 2021; Gendron et al., 2020; Lindquist et al., 2022; Mesquita et al., 2017; Qu et al., 2021).

Critically, constructionist theories of emotion hypothesize that the acquisition and use of emotion concept knowledge is supported by language. Ample evidence, for example, suggests that children's developing understanding of their own and others' mental states is predicated on their parents' use of emotion words (see Ganea & Harris, 2010; Harris et al., 2005; Shablack & Lindquist, 2019). Indeed, a caregiver's emotion word use has been shown to predict their children's emotion knowledge (MacCormack et al., 2020; Thompson et al., 2020). Thus, the transmission and acquisition of emotion knowledge is critical for a social species like human beings given that language can serve as context for emotion-related phenomena and, consequently, aid predictions related to emotion (e.g., Doyle et al., 2021; see also Shablack & Lindquist, 2019).

Once acquired, linguistic emotion concepts can serve as a context for emotion in several ways. First, the words individuals use to describe their emotions can influence how they experience them (Nook et al., 2015; Satpute & Lindquist, 2021). For example, there is evidence to suggest that labeling emotions can decrease (Torre & Lieberman, 2018) or increase (Nook et al., 2021) their intensity, and that people who struggle to verbalize their emotions show behavior that is less context-specific (X. Li et al., 2023; Nook et al., 2015; Preece et al., 2022) and adaptive (Leweke et al., 2012; Preece et al., 2022; G. J. Taylor & Bagby, 2004; Weissman et al., 2020). Furthermore, language can shape the way individuals interpret and make sense of a person's emotions. Different languages have different words and phrases for describing emotions, and these words and phrases can convey different meanings and connotations (Jackson et al., 2019; Zhou et al., 2021). For example, the word "sad" in English can be translated as "triste" in Spanish, "tristeza" in Portuguese, or "حزن" in Arabic, each of which conveys a slightly different meaning and connotation to the observer (Alqarni & Dewaele, 2020; Kayyal & Russell, 2013; Matsumoto, Anguas-Wong, et al., 2008). Lastly, a distinction can be made between a foreign language and a native

language: Foreign languages are typically learned in academic settings rather than being used in everyday situations as with native languages (e.g., Caldwell-Harris, 2014). This restricted contextual diversity associated with the use of a foreign language reduces the emotional valence of abstract words—such as *happy* (see Kousta et al., 2011)—during foreign language use; as a result, individuals report feeling less emotionally reactive when using a foreign language during emotion perception and experience compared to their native language (Ivaz et al., 2016; Matsumoto, Anguas-Wong, et al., 2008; Puntoni et al., 2009).

Finally, language provides a context for the neural basis of emotion. For example, labeling facial portrayals of emotion with emotion words has been found to reduce amygdala activity (Torre & Lieberman, 2018). In contrast, a meta-analysis of emotion perception studies found that the absence of emotion words in fMRI tasks is associated with increased activation in the amygdala (Brooks, et al., 2017). Given the amygdala's role in salience and uncertainty detection (Adolphs, 2010), it is probable that the absence, versus presence, of emotion words renders evocative stimuli as more salient and uncertain because of their relative ambiguity. On the other hand, the presence of emotion words means greater accessibility to conceptual knowledge about emotional states, and thus a greater understanding of the immediate context.

Altogether, culture and linguistic concepts serve as important contexts for understanding one's own and others' emotions. Culture influences how individuals experience and express emotions, as well as how they interpret and make sense of them. Cultural neuroscience studies also show that culture has an effect on the neural basis of emotion perception and regulation. Moreover, linguistic concepts, acquired through language, shape individuals' emotional experiences by influencing how they label and interpret emotions. Language also plays a role in the neural basis of emotion, as the presence or absence of emotion words affects brain activity associated with emotion perception and experience. Although both culture and language function as contextual frameworks for human emotions, their combined effect as forms of context on the brain basis of emotion is yet to be examined. The present dissertation addresses this combined effect on the brain basis of emotion perception.

Situational Effects on Emotion

There is evidence to support the notion that emotions are experienced differently depending on the situation in which they occur. Prior research has shown, for example, that in the presence of others—that is, in *social contexts*—adult participants reported experiencing emotions more intensely (e.g., Jakobs et al., 1996) and the need to regulate emotional states more frequently (e.g., English et al., 2017), than in the absence of others, or *nonsocial contexts*. Other work has suggested that social contexts—whether real or imagined—evoke greater expressive facial behavior than nonsocial contexts, and that social contexts also seem to be a better predictor of expressive behavior than the actual feelings linked to that behavior (Aviezer et al., 2017; Z. Chen & Whitney, 2019; Fridlund, 1991). Indeed, a meta-analysis spanning 69 studies with a total of 3,847 participants and 110 effect sizes for the co-occurrence of specific emotional experiences—happiness, sadness, anger, disgust, fear, and surprise—and their predicted paradigmatic facial signals, revealed an average co-occurrence effect size of .13 (Durán & Fernández-Dols, 2021). These results suggest there is no single link between the experience of a specific emotion category and its corresponding behavioral manifestation, which aligns with the theoretical framework that informs the present dissertation: Different situational instances of an emotion category afford different emotional behaviors for that category (Aldao, 2013; Barrett et al., 2022; Collardeau et al., 2022; Greenaway et al., 2018; Kring & Campellone, 2012; Maren et al., 2013; Mesquita et al., 2017; Scheer, 2012; Uchida et al., 2022; Zhou et al., 2021).

Existing evidence is also suggestive that autonomic nervous system (ANS) responses, such as heart rate, blood pressure, and muscle tension, associated with specific emotion categories are context-dependent. For example, in a classic study by Stemmler et al. (2001), female participants were either experimentally induced to experience anger or fear, or instructed to re-imagine prior events that induced experiences of anger or fear. In the experimental emotion induction condition, for example, the experimenter either quarreled with the participants to evoke anger or, to evoke fear, instructed participants to deliver a public speech that was recorded and evaluated for verbal intelligence; in contrast, in the imagery emotion induction condition, participants were instructed to “relive” actual past events that induced either anger or fear. Both emotion induction methods were successful, but their effects on participants’ ANS responses showed context-specificity. That is, ANS responses varied both by emotion

categories and the induction methods used (Stemmler et al., 2001), suggesting that a person's ANS responses associated with a specific emotion category require modeling the context from which those responses emerged to decode additional, meaningful information about them.

A more recent study echoed Stemmler et al.'s seminal findings on context-specificity of ANS effects. Specifically, McVeigh et al. (2022) had participants undergo three distinct fear-evoking situations involving spiders, heights, or other people, and ANS responses were collected during each fear-evocative situation. The research group found situation- and person-dependency in the relationship between fear and each of their ANS measures, suggesting, again, that autonomic correlates of emotion—here, fear—are context-dependent (McVeigh et al., 2022). These findings are ultimately constituent with a meta-analysis that examined ANS responses associated with specific emotion categories—anger, disgust, sadness, fear, and happiness—across 202 studies. The meta-analysis revealed weak evidence for consistent or specific patterns of ANS changes within each emotion category, indicating that behavioral experiments on emotion show significant variation within emotion categories that is likely tied to situational demands (Siegel et al., 2018).

The impact of situations on emotion have been best-studied in the domain of emotion perception (for a review, see Aviezer et al., 2017). Situation-based contextual influences on emotion perception have been studied using various methods, such as manipulating scenes, body posture, sentences, and narrative storylines. These studies consistently show that context significantly affects the perception of emotional faces. For example, in a classic study by Carroll and Russell (1996), participants were more likely to perceive the emotion anticipated from the situation in a narrative storyline than the one allegedly signaled by an image of posed facial behaviors (e.g., a person posing a putative expression of anger was more likely to be judged as afraid by participants when paired with a story about a frightening situation). Such “situational dominance” (Carroll & Russell, 1996), has been replicated across other methods with other contexts and facial expressions (e.g., Aviezer et al., 2017; Chen & Whitney, 2019, 2022). For example, when naturalistic facial behaviors made by tennis players who have won a tennis match are seen without context, participants are more likely to view the facial expressions as evidence of unpleasantness (Aviezer et al., 2012; see also Barrett, 2022 for a discussion).

The few studies in affective neuroscience that have examined context effects have shown that neural activity associated with emotion also depends on the situation. For example, one study found that fMRI activity associated with the same emotion category, such as anger, depended on whether the emotion was experienced in a physical danger condition or social evaluative condition (Wilson-Mendenhall et al., 2011). In the case of fear, for example, participants' blood-oxygen-level-dependent (BOLD) activity showed specificity to the situational condition, with approximately half of the voxels being unique to a particular situation. In situations of physical danger, participants' experience of fear was related to bodily harm, and was thus more likely to be associated with activation in regions involved in action planning, interoception, and auditory processing; in comparison, in situations of social evaluation, participants' experience of fear was related to negative judgment, and was thus more likely to be associated with activation in regions involved in evaluating oneself and others, accessing social knowledge, regulating oneself, and visualizing details (Wilson-Mendenhall et al., 2011; see also Y. Wang et al., 2022).

Although it did not specifically manipulate context, another recent study found that participants induced to feel emotions that were similar in valence, arousal, and intensity—that is, anger and anxiety—could nonetheless be inductively split into groups defined by distinct patterns of directed functional brain connectivity (Doyle et al., 2022). Participants in said study underwent fMRI while listening to unpleasant music and self-generating experiences of anger and anxiety. Doyle et al. then used an algorithm with unsupervised classification known as s-GIMME (subgrouping Group Iterative Multiple Model Estimation; Gates et al., 2017; Gates & Molenaar, 2012) to identify the presence of statistically differentiable patterns of connectivity associated with the emotion induction conditions. First, the analyses revealed consistent patterns of activation in which s-GIMME reliably classified participants' connectivity patterns based on the experimental emotion induction procedure—that is, brain states that emerged from the anger (vs. anxiety) condition were classified as anger (vs. anxiety). Second, and most pertinent to the present dissertation, s-GIMME identified variability in the functional connectivity patterns associated with experiences of anger and anxiety. For example, in the case of anger, s-GIMME revealed two major subgroups of participants whose connectivity patterns for anger differed significantly, yet their self-reported intensity of anger, anxiety, or arousal did not differ between the subgroups (Doyle et al., 2022). As stated earlier, a

constructionist view of emotion hypothesizes that variation exists in the neural mechanisms associated with the experiences of the same emotion category, reflecting variation in the instances from which those experiences emerged. Indeed, studies have shown that emotion categories each describe populations of highly variable instances (e.g., Durán & Fernández-Dols, 2021; Lindquist et al., 2012; Siegel et al., 2018; Wager et al., 2015). Doyle et al. (2022) did not specifically manipulate the situations in which emotions occurred so could therefore not weigh in on whether different subgroups were related to participants envisioning variable instances of anger (e.g., anger at a romantic partner vs. anger during a sports competition vs. anger when being cutoff in traffic). The present integrative dissertation does so in one of its three proposed studies.

The Integrative Dissertation

The extant behavioral and neuroscientific literature on emotion is suggestive that situational, cultural, and linguistic context should influence the brain basis of emotions, yet very little work has specifically manipulated these factors and tested their effects on the brain basis of emotions. The studies that comprise this integrative dissertation therefore examine how context relates to the brain basis of emotions by manipulating some combination of the situation in which emotion perception and experience occur, the cultural background of the experiencer, and the experiencer's emotion concept accessibility. Specifically, the experimental paradigms used by the studies in the integrative dissertation examined the perception of emotion and the experience of emotion within a sample of Chinese Asian and White American young adult participants. Study 1 uses functional connectivity methods and Study 2 uses univariate methods in the analysis of context effects on the brain basis of emotion, whereas Study 3 proposes directed functional connectivity and subgrouping approaches to the analysis of context effects on the brain basis of emotion.

I designed, implemented, and conducted the parent study (Advancing a situated neuroscience of emotion) that provided the data for the three dissertation studies herein. Specifically, 51 participants were recruited from UNC's campus to partake in a 1.5 hr fMRI study. Participants were Western, non-Hispanic White Americans and Eastern, Chinese Asian individuals who were relatively newly arrived to the United States from mainland China (on average, they had lived in the US for 21 months; in contrast, White Americans were born and had lived their entire lives in the US). During scanning, participants completed

two fMRI tasks. First, participants viewed evocative images that varied in sociality (i.e., whether others were present or absent in the evocative stimuli) and were standardized to evoke, on average, sad and fearful states. This first task supplies data for Study 2 and Study 3. In the second fMRI task, participants viewed facial displays of emotion that are stereotypical of the emotion categories anger and disgust in the United States. Faces were preceded by linguistic emotion labels (i.e., labels for the expressed emotions) or control labels (i.e., no emotion labels). This second task supplies data for Study 1. All three studies test the hypothesis that the neural representation of emotion are influenced by some combination of situational, cultural, and linguistic context.

Study 1 built on prior research suggesting that access to emotion category words, such as “anger,” facilitates access to such emotion concept knowledge and in turn facilitates emotion perception (Doyle & Lindquist, 2018; Gendron et al., 2012; Lindquist et al., 2006, 2014; Nook et al., 2015). Study 1 therefore investigated the impact of cultural influence and emotion concept accessibility on the neural correlates of emotion perception. Across four fMRI runs, Chinese Asian and White American participants were primed with either English emotion category words (anger, disgust) or control text (XXXXXX) before viewing images of White American actors posing facial muscle configurations that are stereotypical of anger and disgust in North American culture. Using a functional connectivity approach, results show that relative to White American participants, Chinese Asian participants showed a significant decrease in connectivity between a region associated with semantic retrieval (the inferior frontal gyrus) and regions association with semantic processing, visual perception, and social cognition, when primed with an emotion category than when primed with a control, meaningless text (XXXXX). These findings suggest a differential benefit of emotion concept accessibility based on participants’ cultural background, and further support the importance of culture as a form of context in emotion perception.

Study 2 tested the hypothesis that brain activity associated with discrete emotional experiences depends on the situational and cultural context in which those experiences occur. Study 2 used standardized evocative stimuli that varied in terms of situation (social v. nonsocial) to induce fear, sadness, and neutral emotional experiences in Chinese Asian and White American participants while undergoing fMRI. Culture here was operationalized in two ways: participants’ self-reported race and national origin functioned as a discrete form of cultural context, whereas participants’ self-reported

perception of United States social norms functioned as a continuous and subjective form of cultural context. Using a regions of interest approach, results support the hypothesis that brain activity associated with discrete emotional experiences depends on the situational and cultural context in which those experiences occur, indicating that brain representations of emotions are context-dependent.

Study 3 extends the prior two studies by using data-driven analyses to inductively generate hypotheses for a situated neuroscience of emotion. Study 3 uses directed functional connectivity and algorithmic subgrouping methods to classify the brain states of individuals to determine which experimental factors—emotion, situation, culture, or a combination of these factors—best characterize the observed patterns of brain connectivity. Specifically, the use of directed functional connectivity to assess the statistical dependencies between brain regions during emotion experience may identify pathways associated with the interaction between different brain areas and grouping of distinct functional connectivity patterns based on contextual factors, such as emotion category (fears vs. sadness), cultural background (Chinese Asian vs. White American), situational context (social vs. nonsocial), or an interaction of these factors. These methods to analyzing functional neuroimaging data have been used previously to study how the brain processes and integrates various forms of information in varying contexts, including risk-taking contexts (McCormick et al., 2019), affective contexts (Doyle et al., 2022), and clinical contexts (Woody et al., 2023). Results from Study 3 were defended during the final dissertation defense.

CHAPTER 2: LANGUAGE ACCESS DIFFERENTIALLY ALTERS FUNCTIONAL CONNECTIVITY DURING EMOTION PERCEPTION ACROSS CULTURES

Introduction

Emotion perception—or understanding the emotional meaning of someone else's facial, body, or vocal behaviors—is crucial to social communication, drives social behavior, and facilitates the social connection that is ultimately critical to human health and wellness (Atzil & Gendron, 2017; LoBue et al., 2019; Milojevich et al., 2021; Telzer et al., 2014). Basic emotion theory classically posits that universal basic emotions are perceived reflexively in others' facial configurations based on feature detection alone (Ekman & Friesen, 1971; Keltner et al., 2019; Scarantino & Griffiths, 2011), yet accumulating evidence suggests that emotion perception depends on conceptual knowledge about emotion that is activated in the minds of perceivers (Barrett et al., 2019; Hassin et al., 2013; Lindquist & Gendron, 2013). Furthermore, evidence suggests that this knowledge is influenced by a person's prior experiences (e.g., Halberstadt et al., 2009), including their cultural background (Gendron et al., 2020; Lindquist et al., 2022). Moreover, growing evidence suggests that immigrants' exposure to a host culture influences their conceptual knowledge about emotions (Gendron et al., 2020) that informs the experience of emotion (De Leersnyder, 2017) and the perception of emotional facial behaviors (Bjornsdottir & Rule, 2021). Thus, the purpose of this preliminary study was to examine for the first time whether brain connectivity patterns during perception of emotional faces are a product of two important sources of conceptual knowledge: emotion concept accessibility and one's cultural background. Specifically, we tested whether emotion words and participants' cultural background alter functional connectivity between regions implicated in semantic retrieval, visual perception, and social cognition during emotion perception.

The availability and accessibility of emotion concept knowledge significantly influences emotion perception (Barrett, 2017, 2022; Barrett et al., 2011; Lindquist, MacCormack, et al., 2015; Lindquist & Gendron, 2013; Nook et al., 2017; Satpute & Lindquist, 2021). An emotion concept such as “anger” represents a set of highly variable, situated instances—for example, anger during a fight with a spouse versus anger at a slight by a boss versus anger when the cat pees on the bed—that are grounded by

modality-specific information tied to the situations in which they occur (e.g., distinctive physiological patterns; Kreibig, 2010; Siegel et al., 2018). According to constructionist models of emotion, emotion concept knowledge is supported via domain-general processes such as abstraction, categorization, and language (Barrett, 2017; Lindquist et al., 2022; Satpute & Lindquist, 2019; see also Xu et al., 2021). Our theoretical framework proposes that emotion category words or concepts such as “anger” serve as placeholders that cohere together otherwise highly variable situated instances as members of the same category (e.g., Atzil & Gendron, 2017; Doyle & Lindquist, 2018; Hoemann et al., 2019; Hoemann & Barrett, 2019; Wilson-Mendenhall et al., 2011).

Behavioral evidence is consistent with the hypothesis that emotion words support access to emotion concept knowledge, and, in turn, alter the perception of facial muscle configurations (see Satpute & Lindquist, 2021). First, access to emotion words can induce categorical perception for emotional facial behaviors. For example, perceivers who learned to pair chimpanzee facial muscle movements with nonsense words subsequently perceived categorical distinctions between facial behaviors that varied dimensionally in their facial muscle configurations (Fugate et al., 2010). These novel category representations can then shape future perceptions. For example, learning to pair novel “alien” facial muscle configurations with a nonsense word caused participants to see a subsequent category exemplar as more similar versus distinct from the learned faces. This effect was significantly reduced when novel “alien” facial muscle configurations were initially learned in the absence of nonsense labels (Doyle & Lindquist, 2018). Second, accessibility to emotion words alters the speed and quality of emotion perception. For example, temporarily impeding access to emotion category words leads to slower and less accurate emotion perception when compared to trials on which emotion category words are accessible to perceivers (Gendron et al., 2012; Lindquist et al., 2014). In contrast, priming emotion words leads to faster perceptions that are biased towards category prototypes when compared to trials in which faces are seen without an emotion word (Halberstadt et al., 2009; Nook et al., 2015).

Meta-analyses of human neuroimaging research also show that emotion perception consistently recruits neural regions associated with semantic processing (e.g., Lindquist et al., 2012; Sabatinelli et al., 2011). In particular, in a meta-analysis assessing the impact of emotion words on emotional face processing, Brooks et al. (2017) found that the mere presence of emotion words—such as “anger” or

“disgust”—in instructions or as response options in neuroimaging tasks, was associated with greater activity in regions associated with semantic retrieval during subsequent exposure to emotionally evocative stimuli. These findings suggest that the mere presence of emotion category words, even in task instructions or response options throughout a task, can prime participants with access to emotion concept knowledge during the processing of emotional stimuli (see also Koban et al., 2017). In contrast, during experimental tasks in which emotion words were absent as compared to present, or when gender as compared to emotion judgments were made about faces, Brooks et al. (2017) found increased BOLD activation in the bilateral amygdala extending into the parahippocampal gyrus. These findings are consistent with the hypothesis that words serve as context for interpreting emotional faces (Lindquist & Gendron, 2013; see also Scherer & Fontaine, 2019) insofar as amygdala activation has been associated with representing salience (e.g., Cunningham & Brosch, 2012) and parahippocampal activation has been associated with using context to make meaning of visual objects (Aminoff et al., 2013; Bohbot et al., 2015). More broadly, these findings are consistent with work on “affect labeling,” showing that access to emotion words reduces amygdala activity and the emotional impact of faces during emotion perception (see Satpute & Lindquist, 2021 and Torre & Lieberman, 2018 for reviews).

Importantly, emotion categories and the conceptual knowledge they afford differ across cultures (Gendron et al., 2012; Kitayama et al., 2006; see also Mesquita et al., 2017), and even emotion words considered to be translational equivalents with English emotion categories, such as anger, fear, and happiness, vary significantly in meaning across languages spanning the globe (Jackson, Watts, et al., 2019). This cross-linguistic variation in emotion category meaning likely exists because different cultural groups evolved in different ecologies and developed different meanings around common emotionally evocative situations (Gendron et al., 2020; Lindquist et al., 2022; Uchida et al., 2022; see also Uchida et al., 2020 and Q. Wang, 2021). Indeed, different cultural groups associate the same emotion category word, such as “anger,” with different facial configurations (Jack et al., 2012; see also Fang et al., 2018) and produce different facial muscle movements both when posing instances of facial expressions associated with those categories and when spontaneously experiencing instances of those emotion categories (Fang et al., 2022). These conceptual differences in emotion perception are also reflected as different neural patterns when individuals from Japan versus the United States perceive posed facial

configurations of emotion (Brooks et al., 2019). More generally, there appear to be culture-based differences in how people process emotional facial behaviors. For instance, past research shows that whereas White participants residing in Japan showed increased activity in the amygdala to White faces posing fearful expressions, Japanese participants residing in Japan showed increased activity in the inferior frontal gyrus (Moriguchi et al., 2005). Relatedly, White American participants residing in the United States and Japanese Asian participants residing in Japan showed greater activity in the amygdala to fearful expressions posed by members of their own culture (Chiao et al., 2008). Collectively, these findings suggest that the presence of emotion words and the cultural background of individuals may interact to predict the neural basis of emotion perception. No study to our knowledge, however, has specifically addressed this question.

The present study tested for the first time whether priming emotion words such as “anger” alters functional connectivity during emotion perception in Chinese Asian and White American participants residing in the United States. We specifically recruited Chinese Asian individuals who were born and raised in mainland China but now reside in the United States, and non-Hispanic White American individuals who were born and raised in the United States. Participants viewed facial muscle configurations posed by White actors that are stereotypical of the English language emotion categories anger and disgust while undergoing fMRI. Faces portraying behaviors stereotypical of anger and disgust in the United States were used because these emotion categories are both perceived to be associated with unpleasant and highly aroused affective states, and share in the activation of multiple facial muscle groups (see Nook et al., 2015 for a discussion). Emotion concept knowledge may be especially important to the understanding of emotional facial portrayals in such contexts where the portrayals do not differ in valence or arousal (see Lindquist et al., 2016, Shablack & Lindquist, 2019, and Widen, 2013 for discussions). Choosing faces with similar muscular activation also allowed us to ensure that brain differences were not merely a product of differences in statistical regularities present in the stimuli.

Across four counterbalanced blocks, posed expressions of anger or disgust were either preceded by the relevant English emotion category word or non-emotional, non-word control text (XXXXXX). English language emotion categories and associated posed facial behaviors were used with the expectation that English emotion words would differentially impact the emotion perception of Chinese

Asian participants, who in the absence of priming, might have relatively less accessibility to English language emotion concept knowledge, including the specific facial muscle configurations stereotypically associated with those categories in a United States context (see Fang et al., 2018). Moreover, White actors were used to mimic the majority racial and ethnic identities in the United States. All target actors were self-identified females; we used all female faces since these poses had the highest normed perceiver agreement for the emotion category depicted in the database we used.

Following on the meta-analytic findings of Brooks et al. (2017), we assessed whether the mere presence of emotion category words preceding perception of posed emotional facial behaviors would impact functional connectivity between the left inferior frontal gyrus (IFG) and bilateral amygdala, as well as connectivity of those regions with 70 other regions linked meta-analytically to semantic processing (e.g., Binder & Desai, 2011; Price, 2012), emotion perception (e.g., Lamm et al., 2011; Sabatinelli et al., 2011; S. F. Taylor et al., 2012) and social cognition (e.g., Pintos Lobo et al., 2023; Van Overwalle, 2009). Analyses were corrected for multiple comparisons using the false discovery rate.

According to some accounts of emotion perception (e.g., see Ekman & Cordaro, 2011), the mere presence of an emotion category label would have no effect on functional connectivity, nor should it interact with the cultural background of a perceiver to influence perception of so-called universal facial expressions of emotion. On the other hand, constructionist accounts of emotion suggest that a word naming an emotion concept activates a cache of conceptual knowledge about the types of instances that populate that category (e.g., see Barrett, 2006). Even if category words such as “anger” and “disgust” have direct translations in other languages, they may be associated with different facial muscle movements across people from different cultural backgrounds (e.g., Jack et al. 2012). We thus hypothesized that priming English language emotion categories might differentially impact functional connectivity while Chinese Asian participants raised in China versus White American participants raised in the United States perceived emotional faces. In particular, we hypothesized that access to English emotion category words might have a larger impact on the functional connectivity of Chinese Asian participants since they might be less familiar with or have less accessibility to English language emotion concept knowledge. We did not have specific hypotheses regarding the impact of labels on perception of specific emotion categories.

Methods

Participants

Fifty-one young adults consented for the overall study, but only 45 participated due to time constraints. All participants were right-handed and denied any history of neurological or psychiatric disease. Participants consented to the study as approved by the UNC Institutional Review Board and were compensated \$50 for their involvement. Four participants were excluded due to head motion exceeding 2 mm. Four additional participants were unable to complete the scanning session in the time allotted due to experimental errors. One other participant requested to leave the scanner mid-scan due to claustrophobia. Thus the final count of participants in this study was 36, comprising 15 Chinese Asian participants ($M_{age} = 20.4 \pm 2.2$; 6 self-identified males) and 21 White American participants ($M_{age} = 22.3 \pm 3.4$; 11 self-identified males). There were no age differences between self-identified female and male participants ($b = -0.03$, $SE = 1.47$, $t = -0.02$, $p = 0.983$), between the two cultural groups ($b = 0.13$, $SE = 1.32$, $t = 0.10$, $p = 0.920$), or between self-identified male and female participants within cultural groups ($b = 3.15$, $SE = 1.92$, $t = 1.64$, $p = 0.111$).

White American participants were born and raised in the United States by primarily monolingual English-speaking non-Hispanic White American-born parents, and all denied ever residing outside of the United States. In contrast, Chinese Asian participants were born and raised in provinces of mainland China excluding areas with significant Western influence, such as Hong Kong, Macau, and Taiwan. These participants were raised by primarily monolingual Mandarin-speaking Chinese-born parents, and all denied ever residing outside their provinces prior to arriving in the United States as adults. In addition, given that Chinese Asian participants had resided in the United States for an average of less than 20 months ($M_{months} = 18.4 \pm 15.1$), they were required to undergo the Test of English as a Foreign Language (TOEFL; Educational Testing Service) to assess their proficiency in English communication. All Chinese Asian participants demonstrated the highest level of proficiency in reading, listening, speaking, and writing in English ($M_{TOEFL} = 107.6$; range = 102-112). There were no significant differences between self-identified Chinese Asian female and male participants in terms of their duration of stay in the United States ($F_{(1, 13)} = 0.02$, $p = .879$) or TOEFL scores ($F_{(1, 13)} = 0.34$, $p = .572$).

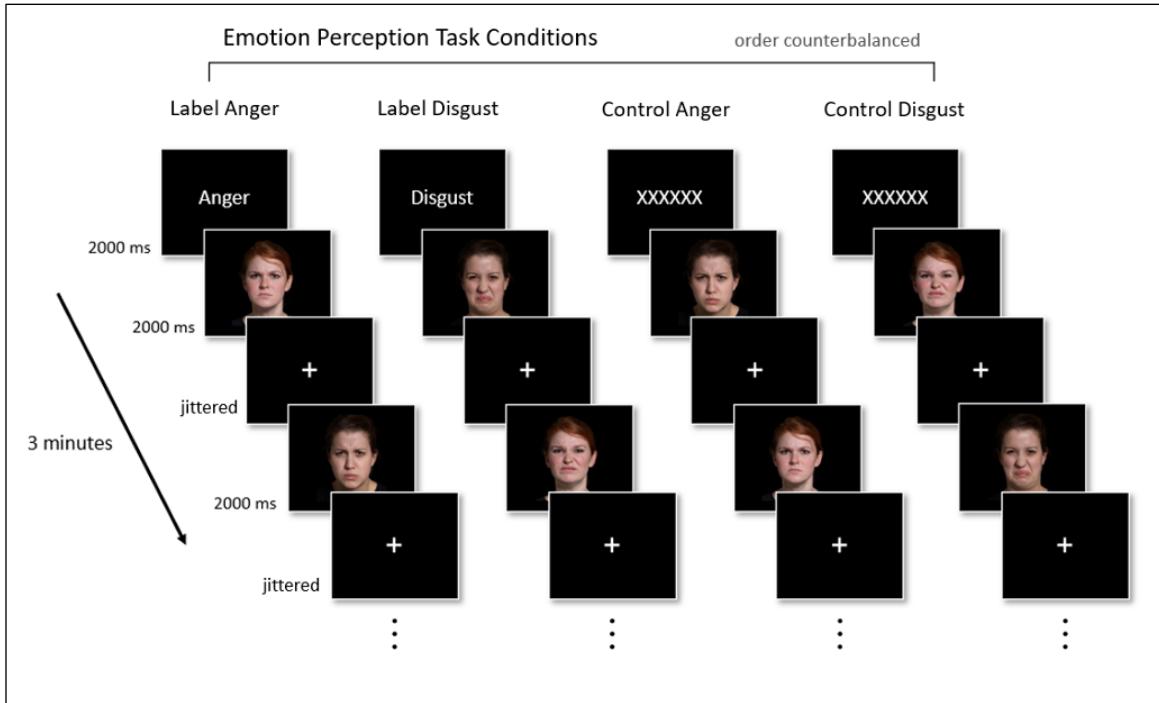
Practice Task

All participants underwent two practice runs of the fMRI task outside the scanner on a laptop computer. These practice runs were identical to the actual fMRI task with the exception of the emotion labels and posed emotional facial portrayals that were used; we opted to use the category “sadness” so as not to impact participants’ perceptual representation of posed angry and disgusted faces prior to seeing them in the scanner. The first practice corresponded to the emotion-word label condition and participants saw the word “Sadness”, after which they passively viewed images of actors portraying facial muscle configurations stereotypical of sadness in the United States. The second practice run corresponded to the control condition. This practice run was exactly like the first but the emotion label was replaced with a control text with no semantic meaning: “XXXXXX”.

Study Design

Participants underwent four 3-minute fMRI runs in a 2 (Emotion: Anger vs. Disgust) x 2 (Label: Emotion Label vs. Control Text) block design. In two of the four runs, participants saw one emotion-word label (either “Anger” or “Disgust”) prior to the start of the run. In the other two runs, the emotion word was replaced with a Control Text (“XXXXXX”). In both the Label and Control Text conditions, text was only shown once at the start of each fMRI run in order for the priming effect to remain subtle. Following the Label or Control Text, participants passively viewed images of actors portraying facial muscle configurations stereotypical of anger or disgust in the United States. We assessed passive viewing because we were interested in whether the mere presence of the emotion word label impacted activation in regions involved in semantic retrieval, even when participants were not explicitly asked to render a category judgment about the face at any point in time during the task. Fixation cross stimuli served as interstimulus intervals (ISIs) and remained on-screen for a jittered amount of time. Because we were interested only in conditions in which an emotion word was congruent with the pictured facial muscle configurations, facial configurations stereotypical of anger were only shown in the “Anger” run [Label Anger] and in one “XXXXXX” run [Control Anger]. Similarly, facial configurations stereotypical of disgust were only shown in the “Disgust” run [Label Disgust] and one “XXXXXX” run [Control Disgust]. The four runs were counterbalanced and faces were presented in a random order within each block. See Figure 2.1 for an illustration of the fMRI paradigm.

Figure 2.1: Experimental Paradigm



Note. The two IASLab actors are depicted as required by the IASLab Face set Release Agreement. In the present study, however, we displayed emotive stimuli from ten actors.

Stimuli

Face stimuli were taken from the NimStim Face set (Tottenham et al., 2009) and the IASLab Face set (www.affective-science.org). We selected 10 different faces expressing sadness from the NimStim Face set to be shown during the practice task that occurred outside the scanner. Face stimuli shown in the fMRI emotion perception task were collected from separate data sets in order to control for potential priming effects prior to scanning. For the fMRI emotion perception task, we selected 10 images of actors portraying facial muscle configurations stereotypical of anger and 10 images of the same actor portraying facial muscle configurations stereotypical of disgust from the IASLab Face set. As a result, the same IASLab Face set actor was displayed multiple times, across emotion conditions. All images depicted White women expressing emotions with a closed mouth to reduce the additional impact of race and gender on emotional face representations and, more practically, because White women's posed

facial behaviors had the highest normed inter-rater agreement for the intended emotion category in the database we used.

fMRI Data Acquisition

We used a 3 Tesla Siemens PRISMA whole-body scanner to acquire structural images and fMRI data. The first structural image was a T1*-magnetization-prepared rapid-acquisition gradient echo: slice thickness = 0.8 mm; 208 slices; repetition time (TR) = 2400 ms; echo time (TE) = 2.22 ms; matrix = 320 x 320; field of view (FOV) = 256 mm; voxel size = 0.8 x 0.8 x 0.8 mm³; sagittal plane. The second structural image was a T2*-weighted, matched-bandwidth, high resolution, anatomical scan: slice thickness = 3 mm; 38 slices; TR = 5700 ms; TE = 65 ms; matrix = 192 x 192; FOV = 230 mm; voxel size = 1.2 x 1.2 x 3.0 mm³. The functional images were T2*-weighted echo-planar images: 37 slices; slice thickness = 3 mm; TR = 2000 ms; TE = 25 ms; matrix = 92 x 92; FOV = 230 mm; voxel size = 2.5 x 2.5 x 3.0 mm³.

fMRI Data Preprocessing

fMRI data were preprocessed using SPM12 (Wellcome Trust Centre for Neuroimaging at UCL, London, UK), implemented in MATLAB 2018a (Mathworks Inc., Natick, MA). Volumes were slice-time corrected, realigned to the mean volume to correct for head motion, normalized, and warped into the standard stereotactic space defined by the Montreal Neurological Institute (MNI, 2 mm). We processed image artifacts originating from head movement using the ART- based scrubbing procedure as an artifact removal tool (Nieto-Castanon, 2020). Signal contributions from the white matter, cerebrospinal fluid, linear BOLD signal trends within each session, and micro-head movements (12 parameter estimates: 3 translation, 3 rotation, and their associated first-order derivatives) were regressed out of the data. Finally, the fMRI data were band-pass filtered (0.008–0.09 Hz) and functional images were spatially smoothed using a Gaussian filter kernel (full width at half-maximum = 8 mm) for subsequent ROI-to-ROI analyses.

Generalized Psychophysiological Interaction (gPPI) Analysis

Functional connectivity was analyzed with the CONN toolbox (version 18b; Whitfield-Gabrieli & Nieto-Castanon, 2012) in MATLAB R2019a (Mathworks Inc., Natick, MA) using gPPI. The seeds of interest were bilateral amygdala and left IFG; meta-analytically, the left IFG shows consistent activation across various fMRI studies on emotion perception when emotion concepts, relative to gender concepts, are present in fMRI studies, that is, *emotion words present > gender words present* in emotion perception

fMRI tasks (Brooks et al., 2017). These findings were taken as evidence by Brooks et al. (2017) that emotion perception requires greater access to semantic knowledge than gender perception. In contrast, bilateral amygdala shows consistent activation for the inverse, that is, *gender words present > emotion words present* across various fMRI studies on emotion perception (Brooks et al., 2017). These findings were taken as evidence by Brooks et al. (2017) that in the absence of emotion category words, emotional facial expressions are more ambiguous in meaning.

We used the Schaefer atlas to identify a parcellation for the left IFG seed using peak coordinates from Brooks et al. (2017). We chose the Schaefer atlas for its ability to provide homogeneous and neurobiologically meaningful features of brain organization based on a multiresolution parcellation generated from using both task-fMRI and resting-state fMRI data across diverse acquisition protocols (Schaefer et al., 2018). Because the Schaefer atlas lacks subcortical parcellations, bilateral amygdala seeds were constructed using peak coordinates of amygdala activation from our meta-analysis on the brain basis of emotion (see Lindquist et al., 2012, Table S3). ROIs were constructed as 6 mm spheres using the MarsBarR toolbox for SPM (Brett et al., 2011) centered at the peak coordinates.

Target regions were selected via the CONN toolbox, which uses both the Harvard-Oxford atlas and AAL atlas (Tzourio-Mazoyer et al., 2002) for cortical and cerebellar parcellations. We specifically were interested in regions that, meta-analytically, show consistent activation during semantic retrieval (e.g., Binder & Desai, 2011; Price, 2012), social cognition (e.g., Pintos Lobo et al., 2023; Van Overwalle, 2009), and emotion perception (e.g., Lamm et al., 2011; Taylor et al., 2012; Sabatinelli et al., 2011). Target regions, in no particular order, spanned superior frontal gyrus (bilateral), middle frontal gyrus (bilateral), right inferior frontal gyrus (pars triangularis and opercularis), temporal poles, superior temporal gyrus (bilateral), middle temporal gyrus (bilateral), superior parietal lobule (bilateral), supramarginal gyrus (bilateral), angular gyrus (bilateral), medial prefrontal cortex, anterior cingulate gyrus (bilateral), anterior insula (bilateral), precuneus (bilateral), parahippocampal gyrus (bilateral), lingual gyrus (bilateral), fusiform gyrus (bilateral), and the cerebellum (crux and vermis). Many of these regions are additionally activated during studies of emotion in general (Kober et al., 2008; Lindquist et al., 2012) and emotion perception, in particular (Fusar-Poli et al., 2009).

First-level ROI-to-ROI gPPI analysis was then implemented in CONN to examine how emotion labels (anger, disgust) and control labels (XXXXXX) modulate functional connectivity during emotion perception between seed and target regions. A gPPI analysis computes how functional association strength between a seed region (e.g., IFG) and a target region (e.g., precuneus) covaries with an external or experimental factor, such as task conditions. In CONN, gPPI analysis involves computation of separate multiple regression models for each target region BOLD timeseries; this involves a) all of the selected task effects convolved with a canonical hemodynamic response function (psychological term), b) seed ROI BOLD timeseries (physiological term), and c) the interaction term specified as the product of a) and b) (PPI term). Second-level analyses were then performed to control for multiple comparisons at the level of seeds using parametric statistics based on Gaussian Random Field Theory (Worsley et al., 1998). Cultural group was used as a covariate in the second-level analysis, with a contrast of *Chinese Asian* > *White American* set for each of the seed regions for differences between task conditions, that is, *Anger Label* > *Anger Control* and *Disgust Label* > *Disgust Control*. We used the false discovery rate (FDR) method for correction for multiple comparisons ($p < 0.05$, two-tailed) (Genovese et al., 2002).

Results

Connectivity measures related to emotion perception for anger did not survive standard significance thresholding. We found no difference in functional connectivity between brain regions for label anger relative to control anger, nor differences between cultural groups for anger conditions. This was the case for connectivity between each of the seed regions (bilateral amygdala and left IFG) and all target regions.

We did, however, observe significant differences in functional connectivity between left IFG and the target regions in the *Disgust Label* > *Control Label* for Chinese Asian compared to White American participants (Figure 2.2). Specifically, we found that functional connectivity between the left IFG and regions implicated in visual face perception (bilateral lingual gyrus), mentalizing (vermis IX), and semantic representation (middle temporal gyrus) decreased in the emotion label condition relative to the control label condition for Chinese Asian participants only ($F_{(8,27)} = 2.58$, $p = .031$; $p < .05$, two-sided FDR seed-level correction) (Figure 2.3). Connectivity between the amygdala seeds and target ROIs for disgust did not survive standard significance thresholding.

Figure 2.2: Connectivity Between Left IFG and Target Regions

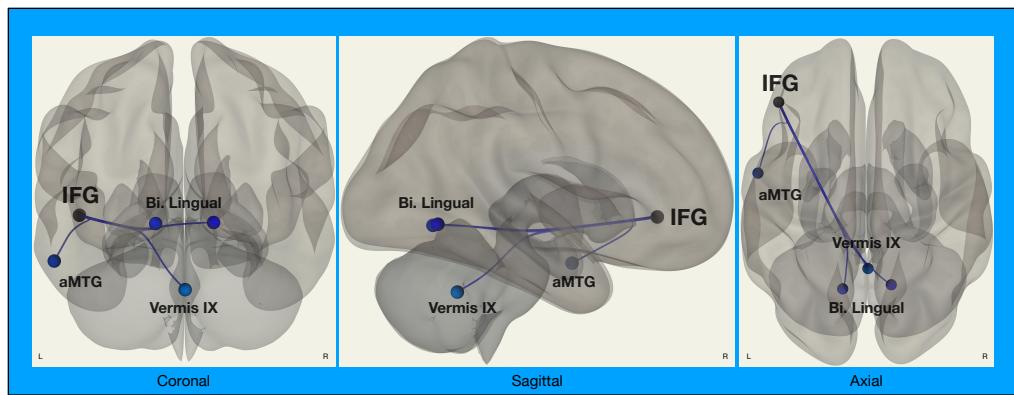
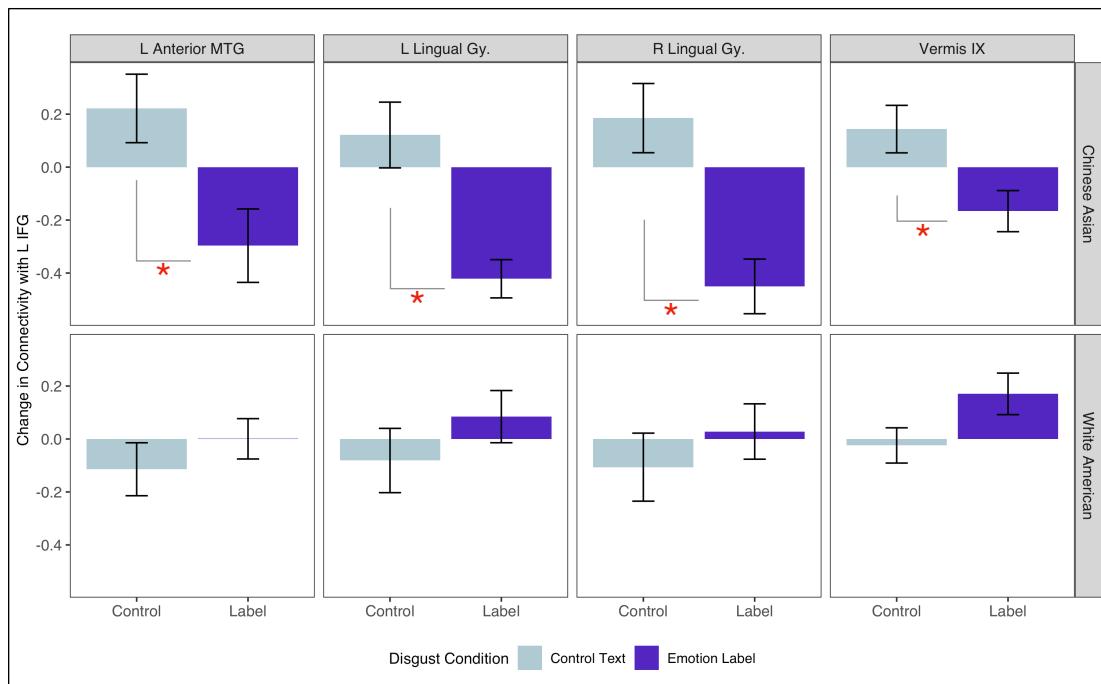


Figure 2.3: Connectivity Differences Between Conditions for the Cultural Groups



Note. Connectivity between the left inferior frontal gyrus (IFG) and the bilateral lingual gyrus (left, $p = .006$; right, $p = .002$), left anterior middle temporal gyrus (aMTG; $p = .029$), and the cerebellum (Vermis 9; $p = .038$). Connectivity measures are corrected for multiple comparisons at the seed-level (FDR-corrected $p < .05$).

Discussion

How culture plays a role in the neural representation of emotion perception—and whether language interacts with culture in this process—is a question of enduring interest in affective neuroscience. Yet very little research has explicitly examined this topic. This preliminary study of 36 participants from the United States and mainland China is one of the first to explicitly examine how access to emotion concept knowledge interacts with a person's culture of origin to impact the neural representation of emotional faces. We based our study on Brooks et al. (2017)'s meta-analysis examining the effect of emotion word priming on the neural representation of emotion perception. The studies represented in Brooks et al. (2017) did not explicitly manipulate the presence or absence of emotion category words in experimental tasks, but, when meta-analyzed, showed that emotion category word accessibility nonetheless influenced the neural representation of emotional stimuli. To follow up on this work, we explicitly primed participants from different cultural backgrounds with English language emotion category word labels before emotion perception. Given the subtle nature of our priming manipulation, and the fact that this study is the first of its kind that we know of, we focused on seed regions of interest observed in Brooks et al. (2017): the left IFG and bilateral amygdala. We found that culture exerted an effect on the functional connectivity between IFG and regions implicated in visual perception, semantic representation, and social cognition when emotion words were primed prior to perceiving faces portraying disgust. This finding suggests that both culture and access to emotion category words may influence how the brain represents emotional facial behaviors during emotion perception. These findings are preliminary given our relatively small sample size and subtle priming manipulation. Nonetheless, they converge with other growing behavioral (Barrett, 2006; Gendron et al., 2012; Lindquist, MacCormack, et al., 2015; Lindquist, Satpute, et al., 2015; Lindquist & Gendron, 2013; Nook et al., 2015; Satpute & Lindquist, 2021) and neural (Brooks et al., 2017, 2019; Brooks & Freeman, 2018) evidence that conceptual knowledge in the mind of perceivers plays an important role in emotion perception.

Cultural Influences on Emotion Perception

The effects of culture on emotion perception found in the present study help to inform the current literature on cultural neuroscience (see Han & Ma, 2014; Shkurko, 2020). In particular, we found that Chinese Asian participants showed decreased functional connectivity between the left IFG and regions

implicated in visual perception, language use, and social cognition when the label “disgust” was presented prior to viewing faces stereotypical of disgust in the United States.

Although we made no predictions about whether specific emotion categories would show differential functional connectivity between the experimental conditions under study, our results are interesting in light of evidence that disgust is expressed (Fang et al., 2022) and perceived (Fang et al., 2018) as less distinctive than anger when comparing Chinese Asian and White European participants. Moreover, translations of “disgust” do not exist in traditional Daoist, Buddhist, or Confucian Chinese texts (Russell & Yik, 1996), suggesting that the category might have been traditionally less central to Chinese culture than to cultural groups descending from Western Europe. Insofar as lingual gyrus activation is associated with face perception (Watson et al., 2016), middle temporal gyrus activation is associated with categorization and semantics (Buckley et al., 1997; Visser et al., 2012), and the vermis 9 of the cerebellum is associated with mentalizing (Van Overwalle et al., 2020), these findings suggest that providing Chinese Asian participants with the English label “disgust” may have reduced the need to engage in more elaborate meaning making of facial behaviors made by White American actors. Although speculative, our findings suggest that in the absence of emotion words, Chinese Asian participants may have been engaging in relatively more visual surveillance of the faces and simulation of the mental state of their posers. In contrast, by priming access to the relevant English category, Chinese Asian participants living in the United States may have been able to merely access the concept of “disgust” to make meaning of the White American disgusted faces.

Limitations and Future Directions

To our knowledge, this is the first study to test these hypotheses and it should thus be viewed as preliminary evidence and a concept proof that language and culture may together influence the neural representation of emotion perception. The current study was limited in multiple ways that should be improved upon in future research. First, we utilized a design that had some strengths: it was, in many ways, a conservative and subtle test of our hypotheses. However, the design also had multiple weaknesses that should be noted. Priming conditions were explicit, albeit subtle; participants were not given expectations for what words meant in the context of the text and they only viewed them for 2 sec before seeing the faces. Nonetheless, the fact that there was an effect of any of the labels—especially on

Chinese Asian participants' brain connectivity—during emotion perception of disgust is suggestive that the prime was sufficient to alter subsequent processing of the faces. Finally, we assessed passive viewing because we were interested in whether the mere presence of the emotion word label impacted activation in regions involved in semantic retrieval, visual perception, and social cognition, even when participants were not explicitly asked to render a category judgment about the face at any point in time during the task. This meant that we could not ensure that participants were actively categorizing the faces as emotional, or even paying attention to them. Again, the fact that we found connectivity differences between the label and control condition when viewing disgust faces suggests that participants were likely paying attention to these faces but future research should include active conditions.

Lastly, we selected our sample to be prototypical of the East-West paradigm commonly used in cross-cultural psychology studies of emotion (e.g., see Mesquita et al., 2017). Yet we sampled individuals of Chinese Asian descent who were living in the United States, which meant they were not completely naive to White American facial emotional expressions. Future studies interested in similar effects of emotion-word labels and culture may find it informative to utilize continuous and/or multiple discrete measures of culture. By selecting participants from a wider pool of Chinese Asians with greater variation in time spent in the US, future research could also examine the amount of time Chinese Asian participants were exposed to Western culture. There is evidence that emotion concept understanding (Jackson, Watts, et al., 2019), facial expressions (Niedenthal et al., 2019), and patterning of emotional experiences (De Leersnyder, 2017), may evolve as a product of cross-cultural contact. Potential future studies may also benefit from incorporating additional conditions such that there are same-race stimuli present for each cultural group and there are labels used in each participant's primary language. Such a paradigm could reveal inter-group biases as well as an additional benefit of labels from participants' primary versus secondary language (e.g., see El-Dakhs & Altarriba, 2018).

Conclusion

Our findings add to growing evidence that conceptual knowledge activated in the minds of perceivers may be essential to the process of emotion perception. In particular, we provide preliminary evidence that brain representations of emotional facial expressions are influenced by two important sources of conceptual knowledge: a person's access to emotion category words and their cultural

background. We assessed the neural processes involved in emotion perception in a sample of Chinese Asian and White American participants living in the United States. Our findings that functional connectivity associated with emotion perception differs as a product of cultural background and access to the host culture's emotion concepts are thus especially relevant in a rapidly globalizing society in which individuals from different cultural groups live in the same context.

CHAPTER 3: SITUATING BRAIN ACTIVITY IN SOCIAL AND CULTURAL CONTEXTS DURING EMOTION

Introduction

Affective science now widely recognizes that social and cultural contexts significantly shape human emotions. Indeed, theoretical accounts and empirical evidence alike support the notion that a person's expression, perception, and experience of emotion are highly influenced by the context in which they occur (e.g., Aldao, 2013; Barrett, 2022; Greenaway et al., 2018; Mesquita et al., 2017; Moore & Depue, 2016; Scheer, 2012; Siegel et al., 2018; Uchida et al., 2022). For example, the meaning and significance of emotional events can vary depending on the social and cultural context in which those events unfold (Benish et al., 2011; Kirmayer & Young, 1998; Manstead & Fischer, 2001; Mesquita & Walker, 2003; Power & Dalgleish, 2015; Smith & Ellsworth, 1985; Uchida et al., 2004). Moreover, individuals use contextual cues to differentiate between different types of emotions, such as fear and anger, and to segment emotional events into discrete units based on contextual differences, such as discerning a fear of heights from a fear of public speaking (Barrett, 2006, 2022; Mesquita et al., 2010; Reisenzein, 2017). Yet the question of how the human brain represents emotional experiences in different contexts remains largely unanswered, despite the extensive evidence of context effects on emotion in behavioral affective science research (Greenaway et al., 2018).

Affective neuroscience has yet to thoroughly examine the role of context on the brain basis of emotions for at least three reasons. First, noninvasive neuroimaging technology such as functional magnetic resonance imaging (fMRI) is a relatively new development for studying affective processes in humans compared to the 150 years of behavioral affective science that preceded it (Gendron & Barrett, 2009). Second, manipulating context in an MRI scanner poses practical difficulties due to the context-limited nature of the scanner environment (cf. Holleman et al., 2020, 2021; Kihlstrom, 2021). Third, the common hypothesis that there are distinct neural systems for specific emotions may deter scientists from prioritizing context as an explanatory variable in the brain basis of emotions (see Fox, 2018; K. M. Lee et al., 2021). Nevertheless, several meta-analyses of the extant literature fail to reveal evidence that there

are neural correlates that both consistently and uniquely activate for a given emotion category (Kober et al., 2008; Lindquist et al., 2012; Wager et al., 2015; Xu et al., 2021; see also Hamann, 2012). The present study contributes to this growing understanding by showing that context is not only relatively simple to operationalize in fMRI design through the use of evocative stimuli and participant sampling procedures, but, more importantly, that context alters the brain activity associated with emotions.

The Role of Context in Emotion

Affective science has traditionally emphasized situational and cultural factors as the primary forms of context that shape emotional events and experiences (e.g., Barrett et al., 2011; Bartz et al., 2011; Carlino et al., 2014; Scherer et al., 2011). Situational factors include both basic perceptual features of the environment, such as the presence of others, whether in-person, depicted, or imagined (e.g., Atzil et al., 2023; Chou & Nordgren, 2017; Wilson-Mendenhall et al., 2011), and abstract conceptual features of the environment that influence behavior, often without a person's awareness of such influence (e.g., Bargh & Pietromonaco, 1982; Shariff et al., 2016). For instance, emotions experienced in social contexts are often experienced more intensely than when experienced alone (Liljeström et al., 2013; Parkinson & Simons, 2009; for reviews, see Fischer et al., 2003 and Niedenthal & Brauer, 2012).

Existing evidence suggests that situational contexts alter the brain basis of emotions. Meta-analytic evidence, for example, has shown that the brain activation associated with affective states differs significantly when the situational context involves sensations targeting different sensory modalities (e.g., vision v. olfaction v. audition; Čeko et al., 2022; Satpute et al., 2015). Other meta-analytic work has shown that the brain activation associated with affective states experienced in social contexts, or in the presence of other humans, differs from those experienced in nonsocial contexts, or in the absence of other humans (Atzil et al., 2023). In Atzil et al. (2023), affective states in social contexts involved increased activation across a swath of the default mode network (involving ventromedial and dorsomedial prefrontal cortex, posterior cingulate cortex and precuneus, lateral temporal cortex, and ventrolateral prefrontal cortex) and the salience network (involving insula, dorsal anterior cingulate cortex, ventral anterior cingulate cortex, thalamus, and amygdala), whereas affective states in nonsocial contexts involved relatively more localized activation in subcortical regions associated with behavioral action, such as the ventral striatum and amygdala.

More specifically, experiences of fear in social contexts, whether actual, imagined, or depicted (e.g., Kaźmierowska et al., 2022; Lindquist et al., 2012; Wilson-Mendenhall et al., 2011), have been associated with brain activation in areas implicated not only in arousal, such as the amygdala (Pessoa & Adolphs, 2010), but also in social cognition (e.g., Lieberman et al., 2019), including the temporal poles, temporoparietal junction, and ventral and dorsal regions of the medial prefrontal cortex. In contrast, experiences of fear in nonsocial contexts have been linked to brain activation in areas associated with spatial processing and behavioral action planning (e.g., Wilson-Mendenhall et al., 2011). Yet even across instances of nonsocial fear, such as heights or encountering spiders, there is variability in brain activation, with no single region consistently associated with self-reports of fear (Y. Wang et al., 2022).

Unlike situational contexts, the cultural context in which emotions occur can shape emotional experiences by operating at multiple levels of analysis, including micro and macro levels of analysis (e.g., see Uchida et al., 2020). Micro-level factors can encompass individual beliefs, values, and socialization experiences, which become implicit and explicit sources of information that individuals use to navigate and interpret situations (Causadias et al., 2018a; Crocetti et al., 2022; Firat, 2021; Lindquist et al., 2022; Mesquita et al., 2017; see also Deng et al., 2019). Racial identity and nationality are examples of micro-level factors that individuals internalize from their cultural milieu (e.g., Nasie et al., 2016; Rizzo et al., 2022). In contrast, macro-level factors are operationalized at the societal level, such as federal, state, or district-level policies, social and political structures, historical events, and cultural norms (e.g., Harrington & Gelfand, 2014; Payne et al., 2019). Macro-level factors influence populations across generations by altering micro-level factors, including individual-level perceptions, attitudes, and emotions (H. Chen et al., 2021; Chua et al., 2019; Jackson, van Egmond, et al., 2019; Liu et al., 2018). For example, historical events such as chattel slavery (Acharya et al., 2016) and federal policies such as antigay legislation (Ofosu et al., 2019) have a lasting impact on micro-level factors, shaping the emotional experiences of events in complex and multifaceted ways (Baldwin & Mussweiler, 2018; Ganzel et al., 2007; see also Q. Wang, 2021).

Most neuroimaging studies on emotion in cultural neuroscience have used cultural group membership, such as nationality or national origin, as a proxy for cultural context and its impact on emotion perception (Han & Ma, 2014; Shkurko, 2020). Emotion perception, however, is a separate

construct from emotional experiences that occur in response to an evocative event (Satpute & Lindquist, 2021). Studies on empathy, which in some operationalizations involves vicarious emotional experiences, support the hypothesis that cultural context can influence the neural activation associated with emotional experiences (Han & Ma, 2014). For example, Han & Ma (2014), in their meta-analysis of cultural differences in functional brain activation, find that White Western participants consistently show greater activation in the ventral anterior insula during social affective processing such as empathy compared to East Asian participants. Insofar as the ventral anterior insula is believed to reflect visceral and autonomic processing of affective states (e.g., Molnar-Szakacs & Uddin, 2022), these findings may suggest greater emotional reactivity in White Western participants relative to East Asian participants during vicarious experiences of emotion. Such theorizing is in fact consistent with extensive behavioral work demonstrating differences in the experience of emotion across cultures, particularly in the experience of negative emotion (e.g., for reviews, see De Vaus et al., 2018; Yoo & Miyamoto, 2018).

Finally, Chinese participants also exhibit differences in the regulation of emotional experiences compared to their White Western counterparts due, in part, to cultural norms reflecting group harmony versus individual expression. For example, East Asian cultural norms typically place greater emphasis on the regulation of emotional expression in social contexts (Novin et al., 2010), and research suggests that Chinese individuals are more likely to use suppression as a habitual strategy for regulating their emotions (Deng et al., 2017; Ji & An, 2021). These cultural differences in emotional experience and regulation are also reflected in neural activity. Chinese participants, compared to White German participants, exhibit greater dorsolateral prefrontal cortex activation during an empathy task, suggesting that they may exert more cognitive control over their emotional responses when viewing others in distress (de Grecq et al., 2012). Additionally, Chinese participants' greater belief that emotions are changeable and their greater tendency to regulate their emotions via reappraisal in daily life (Deng et al., 2017; Ji & An, 2021; Matsumoto, Yoo, et al., 2008) is correlated with relatively less ventrolateral prefrontal cortex activation during an emotion regulation task when compared to White American participants, suggesting that Chinese participants' habitual use of reappraisal may make emotion regulation attempts less effortful (Qu & Telzer, 2017).

Taken together, the available evidence suggests that situational and cultural contexts can alter the neural representation of emotions, but little is known about how these two forms of context interact to influence said representations. To address this gap, we conducted a study in a sample of Chinese Asian and White American participants residing in the United States and examined how situational and cultural factors jointly influence the neural representations of two negative emotions, fear and sadness. This study is the first, to our knowledge, to examine the interaction between situational and cultural contexts in shaping neural activity associated with emotional experiences.

The Present Study

Drawing on theory that emotions are situated instances that correspond to the affordances of the present context (e.g., Barrett, 2017; Mesquita et al., 2010; Satpute & Lindquist, 2019; Siegel et al., 2018; Wilson-Mendenhall & Barsalou, 2016), we conducted a neuroimaging study that integrates the fields of affective neuroscience and cultural neuroscience to examine the extent to which the brain basis of emotions reflects this situatedness. Specifically, we used fMRI to investigate neural responses to unpleasant emotions (i.e., fear and sadness) during specific situational contexts (i.e., social and nonsocial) within the brains of individuals from two cultural backgrounds (i.e., Chinese Asian participants and White American participants). We focused on a set of *a priori* regions of interest (ROIs) generated via a meta-analysis of cross-cultural differences in brain activation during social-cognitive and social-affective tasks (Tables 2 and 3 in Han & Ma, 2014). Many of these same brain regions, however, are active during the experience of emotions (for meta-analyses, see Atzil et al., 2023; Lindquist et al., 2012; Vytal & Hamann, 2010). In Table 3.1 we list the ROIs under study and their connection to relevant prior research.

Manipulating the Situation

We used evocative images depicting, or lacking, other humans to manipulate the sociality of the situational context in which experiences of fear and sadness occurred (see Atzil et al., 2023, for a similar approach). In line with past work (e.g., Wilson-Mendenhall et al. 2011; see Atzil et al. 2023 for a meta-analysis), we predicted that social contexts would elicit greater activation in a set of ROIs including the anterior insula, amygdala, dorsomedial prefrontal cortex, dorsolateral prefrontal cortex, temporal poles, temporoparietal junction, and the medial prefrontal cortex extending into the anterior cingulate cortex (see Table 3.1). Meta-analytic evidence illustrates that these brain regions are collectively involved in the

experience of emotions (Lindquist et al., 2012; Vytal & Hamann, 2010), with amygdala, anterior cingulate cortex, and insula involved in the generation and representation of visceromotor activation (Lindquist et al., 2012; Lindquist & Barrett, 2012; Seeley, 2019; Seeley et al., 2007), and the dorsomedial prefrontal cortex, temporal poles, and temporoparietal junction linked to abstract categorization and representation of one's own current affective state (Satpute & Lindquist, 2019). Critically, the latter regions have also been linked to social cognition and the representation of others' behaviors (Spreng et al. 2009; van Overwalle, 2009) and thus might subserve the generation of affective predictions in the self that reflect others' on-going emotional states. Based on this evidence and evidence that nonsocial instances of emotion involve relatively more activity in brain regions associated with spatial processing and behavioral action planning (Atzil et al., 2023; Qi et al., 2018; Wilson-Mendenhall et al., 2011), we predicted that social versus nonsocial instances of fear and sadness would involve more activation in brain regions associated with the generation of affective states and abstract representation and social cognition. Table 3.1 lists these hypotheses by brain region.

Manipulating and Measuring Culture

In the present study, we operationalized cultural context in two ways. As is common in cultural neuroscience studies (e.g., see Han & Ma, 2014; Shkurko, 2020), we first operationalized cultural context as participants' self-reported race and nationality, which we refer to as *cultural identity* (see Denkhaus & Bös, 2012; Markus & Kitayama, 2010; Martínez Mateo et al., 2012; Morris et al., 2015; Nguyen-Phuong-Mai, 2021; Salter et al., 2018; Salter & Adams, 2016 for critical discussions on cultural identities). Thus participants were selected to join the study because they either self-identified as Chinese Asian or White American adults. A further requirement for enrollment was that participants with a self-identified Chinese Asian cultural identity had been born and raised in Mainland China until at least age 18 and that participants with a self-identified White American cultural identity had been born and raised in the United States and had never lived outside it. We reasoned, like prior theorists that have used the East-West paradigm (e.g., see Kitayama et al., 2020), that participants born and raised in mainland China versus the United States would have been exposed to different macro-level cultural factors such as social norms surrounding emotions (De Vaus et al., 2018; Eid & Diener, 2001; Gendron et al., 2020; Lindquist et al.,

2022; Mesquita et al., 2017; Spencer-Rodgers et al., 2010; Uchida et al., 2022; Yoo & Miyamoto, 2018; see also Collardeau et al., 2022; Telzer et al., 2016).

In line with cultural neuroscience studies (Han & Ma, 2014; Sasaki & Kim, 2017; Shkurko, 2020), we hypothesized cultural differences in regional brain activation within our ROIs. For example, we predicted greater activation in the medial prefrontal cortex extending into the dorsal anterior cingulate cortex (MPFC/dACC) and amygdala for White American participants compared to Chinese Asian participants during emotion experience, based on behavioral evidence indicating that White American participants generally experience emotions as more arousing than East Asian participants (see De Vaus et al., 2018, for a review). Conversely, we predicted greater activation in the dorsomedial and dorsolateral regions of the prefrontal cortex (DMPFC, DLPFC) for Chinese Asian participants compared to White American participants during emotion experience, based on behavioral evidence indicating that East Asian participants both experience emotions as more other-oriented and are more likely to regulate their emotions both implicitly and explicitly than White Westerners (Bebko et al., 2019; Boiger et al., 2012; E. Davis et al., 2012; Deng et al., 2019; L. M. W. Li & Masuda, 2016; Ma-Kellams & Blascovich, 2012; Miyamoto et al., 2014).

In addition to cultural identity, we also measured individual differences in subjective experience of living in the United States as a second operational definition for cultural context. We were interested in assessing individual differences because there was variation in Chinese Asian participants' duration in living in the United States ($M_{months} = 20.88 \pm 15.1$; range = 2 to 52 months). Moreover, we reasoned that the choice to move to another nation versus to remain in one's home nation might reflect differences in underlying psychology amongst our Chinese Asian participants, regardless of their cultural identity. Indeed, there is evidence that voluntary mobility has been linked with holding more individualistic personal values (e.g., Oishi, 2010). We thus investigated individual differences in perceptions of the United States' cultural tightness among both Chinese Asian and White American participants. Cultural tightness refers to the extent to which a society's social norms are perceived to be pervasive, clearly defined, and reliably imposed (Gelfand et al., 2006), and it plays a critical role in shaping an individual's emotional experiences and expressions (Baldwin & Mussweiler, 2018; Liu et al., 2018; see also Sawada & Nomura, 2020). As a form of individual differences in perceptions of social norms, we aimed to

determine whether individual differences in perceptions of cultural tightness of US social norms would influence participants' regional brain activation during emotional experiences. Following newer work that cultural identity interacts with cultural factors like cultural tightness (e.g., see Kraus & Kitayama, 2019), we furthermore conducted exploratory analyses assessing the interaction of these factors on regional brain activation during emotional experiences. We did not make any predictions regarding how cultural tightness would relate to functional brain activation as no prior fMRI study has examined cultural tightness in relation to the brain basis of emotion.

Table 3.1: Regions of Interest, Prior Evidence, and Hypotheses

Region / Location	Function	Social-Affective Neuroscience Insights	Social-Cultural Neuroscience Insights	Hypotheses
Medial prefrontal cortex extending into dorsal anterior cingulate cortex (MPFC/dACC)	Engagement of visceromotor activation and regulation of attention and response-selection (Dixon et al., 2017; Yoshida et al., 2010)	Social contexts and various aspects of social cognition activate the MPFC/dACC (Pfeifer & Peake, 2012; Pintos Lobo et al., 2023). For example, contexts requiring self-reference all activate the MPFC/dACC (Arioli, Cattaneo, et al., 2021; Qin & Northoff, 2011; Vago & Silbersweig, 2012).	White Western participants consistently show greater MPFC/dACC activation during mentalization and self-reference compared to East Asian participants (Han & Ma, 2014; Shkurko, 2020). This finding aligns with extensive behavioral evidence demonstrating cultural variation in phenomena that rely on mentalizing and self-reference, including emotion recognition and experience (Mesquita et al., 2017; Mesquita & Frijda, 1992; Spencer-Rodgers et al., 2010; Uchida et al., 2008), suggesting a neural basis for said variation.	<u>Effect of social context:</u> Across participants, social experiences of fear and sadness will show greater MPFC/dACC activation than nonsocial experiences of fear and sadness. <u>Effect of cultural context:</u> White American participants will show greater MPFC/dACC activation than Chinese Asian participants during emotion experience.

Table 3.1 cont.

Region / Location	Function	Social-Affective Neuroscience Insights	Social-Cultural Neuroscience Insights	Hypotheses
Dorsolateral prefrontal cortex (DLPFC)	Executive functioning, including behavioral and cognitive control	Self-monitoring and the monitoring of others activates the DLPFC (McDonald et al., 2020; Suzuki et al., 2012; Yoshida et al., 2010). For example, emotion regulation and recognition activate the DLPFC (Andò et al., 2021; Mitchell, 2011).	East Asian participants consistently show greater DLPFC activation during emotion perception compared to White Western participants (Han & Ma, 2014; Shkurko, 2020). This pattern of heightened DLPFC activation among East Asian participants is in line with extensive behavioral evidence demonstrating higher levels of implicit and explicit emotion regulation among Chinese Asian participants compared to White American participants (e.g., Deng et al., 2017, 2019; Qu & Telzer, 2017).	<u>Effect of social context:</u> Across participants, social experiences of fear and sadness will show greater DLPFC activation than nonsocial experiences of fear and sadness. <u>Effect of cultural context:</u> Chinese Asian participants will show greater DLPFC activation than White American participants during emotion experience.

Table 3.1 cont.

Region / Location	Function	Social-Affective Neuroscience Insights	Social-Cultural Neuroscience Insights	Hypotheses
Dorsomedial prefrontal cortex (DMPFC)	Abstract categorization; meaning-making	Social information processing activates the DMPFC (Lieberman et al., 2019). For example, (Satpute & Lindquist, 2019) contexts that involve emotion recognition (Dricu & Frühholz, 2016), perspective-taking (Healey & Grossman, 2018), and interpersonal emotion regulation (Phillips et al., 2023; Reeck et al., 2016) activate the DMPFC.	East Asian participants consistently show greater DMPFC activation during mentalization and self-reference compared to White Western participants (Han & Ma, 2014; Shkurko, 2020). This finding is consistent with abundant behavioral evidence indicating that during target judgments, East Asian participants tend to consider the broader social context more than White Western participants (De Vaus et al., 2018; Mason & Morris, 2010; Mesquita et al., 2017; Mesquita & Frijda, 1992; Spencer-Rodgers et al., 2010).	<u>Effect of social context:</u> Across participants, social experiences of fear and sadness will show greater DMPFC activation than nonsocial experiences of fear and sadness.
Right Hemisphere [14, 52, 40]				<u>Effect of cultural context:</u> Chinese Asian participants will show greater DMPFC activation than White American participants during emotion experience.

Table 3.1 cont.

Region / Location	Function	Social-Affective Neuroscience Insights	Social-Cultural Neuroscience Insights	Hypotheses
Ventral anterior insula (vAI NS) Left Hemisphere [-38, 2, -10]	Affective and autonomic processing; representing afferent visceromotor signals from the body (Kurth et al., 2010, p. 20; Uddin et al., 2017)	Social affective experiences, such as empathic concern, consistently activate vAI NS (e.g., Kurth et al., 2010).	White Western participants consistently show greater vAI NS activation during emotion perception compared to East Asian participants (Han & Ma, 2014). This finding aligns with extensive behavioral evidence that links heightened emotional experience with White Western participants relative to East Asian participants (De Vaus et al., 2018; Yoo & Miyamoto, 2018).	<u>Effect of cultural context:</u> White American participants will show greater vAI NS activation than Chinese Asian participants during emotion experience.

Table 3.1 cont.

Region / Location	Function	Social-Affective Neuroscience Insights	Social-Cultural Neuroscience Insights	Hypotheses
Amygdala (AMY) Left Hemisphere [-20, -04, -16]	Salience detection; represents motivational relevance of stimuli	The amygdala shows consistent activation in response to social affective stimuli over nonsocial affective stimuli (Atzil et al., 2023; Frewen et al., 2011; Stanley, Adolphs, 2016).	White Western participants show greater amygdala activation during emotion perception compared to East Asian participants (e.g., P. Chen et al., 2019; Moriguchi et al., 2005). This finding aligns with extensive behavioral evidence suggesting that emotional experiences are more salient to White Western participants than to East Asian participants (e.g., De Vaus et al., 2018).	<u>Effect of social context:</u> Across participants, social experiences of fear and sadness will show greater AMY activation than nonsocial experiences of fear and sadness. <u>Effect of cultural context:</u> White American participants will show greater AMY activation than Chinese Asian participants during emotion experience.

Table 3.1 cont.

Region / Location	Function	Social-Affective Neuroscience Insights	Social-Cultural Neuroscience Insights	Hypotheses
Temporal Pole (TP)	Semantic knowledge retrieval;	Conceptualization fundamentally activates the temporal poles. For example, the ability to recognize faces, interpret events, and understand abstract social concepts such as norms and expectations (Pobric et al., 2007; Ralph et al., 2017; Visser et al., 2012; see also Lin et al., 2018a) activates the temporal poles.	White Western participants show greater TP activation during emotion perception compared to East Asian participants (Han & Ma, 2014). However, since the TP is associated with integrating others' perspectives into one's own experiences (Olson et al., 2007; Pehrs et al., 2017), and East Asian participants tend to explain events, including their own emotional experiences, in a way that more strongly incorporates others' perspectives (e.g., Kitayama et al., 2006), we predict that Chinese Asian participants will show greater TP activation than White American participants during emotion experience.	<u>Effect of social context:</u> Across participants, social experiences of fear and sadness will show greater TP activation than nonsocial experiences of fear and sadness. <u>Effect of cultural context:</u> Chinese Asian participants will show greater TP activation than White American participants during emotion experience.
Right Hemisphere [50, 14, -20]	language comprehension	(Herlin et al., 2021)		

Table 3.1 cont.

Region / Location	Function	Social-Affective Neuroscience Insights	Social-Cultural Neuroscience Insights	Hypotheses
Temporoparietal Junction (TPJ) Right Hemisphere [54, -44, 26]	Monitoring and updating mental representations of the world (Decety & Lamm, 2007; Donaldson et al., 2015; Doricchi et al., 2022)	The ability to infer mental states, including one's own and others' emotions, beliefs, and intentions, is linked to the TPJ (e.g., Bzdok et al., 2012).	East Asian participants consistently show greater TPJ activation during mentalization and self-reference compared to White Western participants (Han & Ma, 2014; Shkurko, 2020). This finding aligns with extensive behavioral evidence showing that East Asian participants' target judgments are more likely to track the social context than that of White Western participants' target judgments (Kitayama et al., 2020; Mason & Morris, 2010; Mesquita & Frijda, 1992; Spencer-Rodgers et al., 2010).	<u>Effect of social context:</u> Across participants, social experiences of fear and sadness will show greater TPJ activation than nonsocial experiences of fear and sadness. <u>Effect of cultural context:</u> Chinese Asian participants will show greater DLFC activation than White American participants during emotion experience.

Note. The regions of interest (ROIs) were selected from the meta-analysis by Han & Ma (2014), except for bilateral amygdala, which were selected from our meta-analysis on the brain basis of emotion (Lindquist et al., 2012). MNI coordinates are provided in brackets as [x, y, z].

Methods

Participants

In the present study, we recruited 51 participants from The University of North Carolina (UNC) at Chapel Hill. Participants were right-handed and denied any history of neurological or psychiatric disease. Participants provided written consent to the study as approved by the UNC Institutional Review Board and were compensated \$50 for their involvement. Six participants were excluded: three due to head motion exceeding 2 mm, two due to failure to respond on more than 10% of trials, and one due to claustrophobia. Thus the final sample was 45 participants comprising 23 Chinese Asian participants ($M_{age} = 20.8 \pm 2.4$) of whom 12 self-identified as female and 11 as male and 22 White American participants ($M_{age} = 21.9 \pm 3.1$) of whom 11 self-identified as female and 11 as male. Chinese Asian participants were born in provinces of mainland China and raised by monolingual Mandarin-speaking Chinese-born parents, and all denied ever residing outside their provinces prior to arriving to the United States as adults. Note that we excluded Chinese Asian participants raised in Hong Kong, Macau, or Taiwan before arriving in the United States, as these regions have had relatively more exposure to Western norms due to their histories of colonization (e.g., see L. Li et al., 2020; Qu et al., 2020). In contrast, White American participants were born and raised in the United States by primarily monolingual English-speaking non-Hispanic White American-born parents, and all denied every residing outside of the United States. Male participants were on average 1.6 years older than female participants ($F_{(1, 41)} = 3.92, p = .054$). No further age differences were observed.

Because Chinese Asian participants had lived in the United States for less than 24 months ($M = 20.8 \pm 15.1$), we used the Test of English as a Foreign Language (TOEFL; Educational Testing Service) ($M = 107.2 \pm 4.5$) to confirm proficiency in spoken and written English. There was no difference in time spent in the United States ($p = .65$) or in TOEFL scores ($p = .12$) between sexes for Chinese Asian participants.

Task and Stimuli

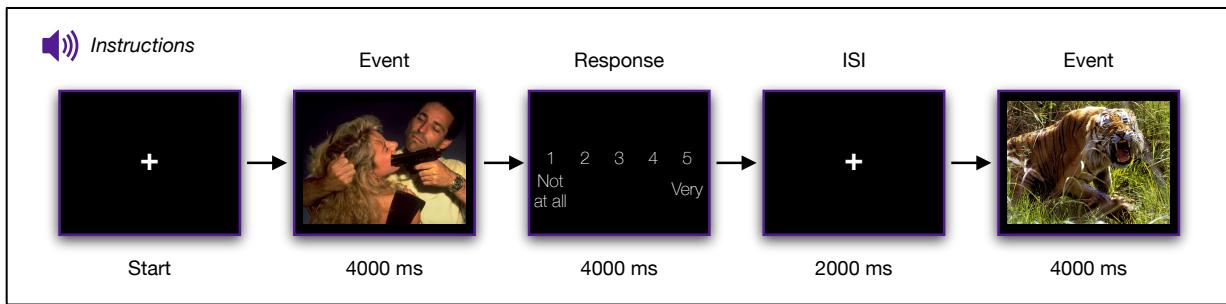
Stimuli from the IAPS and related data sets were used to induce fear, neutral affect, and sadness. One hundred and eighty images were used in the fMRI experiment, resulting in 180 trials or events. Half of these events depicted humans (social context; $n = 90$) and half depicted content devoid of humans

(nonsocial context; $n = 90$). Each set of the situational contexts—social and nonsocial—included fear ($n = 30$), neutral ($n = 30$), and sad ($n = 30$) events. The fMRI experiment comprised five experimental runs.

Per our prior work using electroencephalogram (Pugh, Choo, et al., 2022; Pugh, Huang, et al., 2022), each trial began with a stimulus presentation—fear, sad, or neutral—that lasted 4000 ms. This stimulus event was followed immediately by a response scale whose duration was also 4000 ms. During the response scale, participants used a 5-point Likert-type scale to report their degree of felt intensity in response to the preceding fearful, sad, or neutral event. Participants made these responses using a button box in their right hand. Participants were instructed outside the scanner, and reminded at the beginning of every experimental run, that a value of 1 on the scale (“not at all”) denoted low-to-no reactivity in response to fear, sad, or neutral events, whereas a value of 5 on the scale (“very”) denoted high, intense reactivity in response to fear, sad, or neutral events. Immediately following the response scale was an interstimulus interval (ISI) presentation ($M_{ISI} = 2000$ ms). Please see Figure 3.1 for an illustration of an fMRI trial.

To evoke contextual effects from still images (see Aldao, 2013; Wilson-Mendenhall et al., 2013b for discussions), participants were instructed to imagine experiencing the depicted events from a first-person perspective, as if watching the events unfold before them. Participants were instructed to pay particular attention to their subjective experience of the events, and to use that information to answer the response scales. Participants engaged with the task on a laptop computer during a practice run before entering the scanner. The design of the practice run was identical to the fMRI task but consisted of only one run and exposed participants to disgust and neutral stimuli that varied in sociality. Participants verified they understood the task by explicitly providing reactions to the practice stimuli that were unequivocally related to the depicted events, self-focused, and encapsulated in a value between 1 (low-to-no reactivity) and 5 (high, intense reactivity).

Figure 3.1: fMRI Trial



Note. Participants completed five experimental runs at 6 min per run. Instructions for self-immersion and response scales were repeated to participants before the start of each run. The 2×3 within-subjects design of the experiment—Situation (social, nonsocial) \times Emotion (fear, neutral, sad)—yielded “social-fear” trials (e.g., knife-wielding individuals), “nonsocial-fear” trials (e.g., an impending tornado), “social-neutral” trials (e.g., people walking), “nonsocial-neutral” trials (e.g., landscapes), “social-sad” trials (e.g., people attending a funeral), and “nonsocial-sad” trials (e.g., injured animals). The figure above illustrates a complete social-fear trial with the start of a nonsocial-fear trial.

Manipulation Check: Self-reported Emotion

We used participants’ in-scanner self-reported emotion (i.e., their response scales of felt-intensity) as a manipulation check for the emotion inductions. Specifically, response scales were used to verify that fear and sad events elicited stronger self-reported emotion than neutral events (i.e., *fear > neutral and sad > neutral* in self-reported emotion). Self-reported emotion was analyzed in a multilevel framework using *lme4* (Bates et al., 2015) in the R environment with response scales nested within participant ($k_1 = 45$) and stimulus ($k_2 = 180$). Participants and stimuli were selected as the clustering units or random intercepts since self-reported emotion occurred at these levels (Judd et al., 2012). Degrees of freedom, test statistics, and P values were derived from Satterthwaite approximations in the *lmerTest* R package (Kuznetsova et al., 2017). Planned contrasts (Garofalo et al., 2022) were conducted using *emmeans* (Lenth et al., 2022) in the R environment and corrected using the “mvt” (multivariate t distribution) adjustment for multiple comparisons (Westfall, 1997; Westfall & Tobias, 2007).

Manipulation Check: Perceptions of Cultural Tightness

The tightness-looseness scale (Mu et al., 2015) was used to verify group differences in cultural tightness ($\alpha_{\text{Chinese}} = 0.71$; $\alpha_{\text{White}} = 0.89$; $\alpha_{\text{All}} = 0.88$). Lower scores on cultural tightness indicate stronger perceptions of the United States as a nation that is loose and tolerates deviance from social norms, whereas higher scores on cultural tightness indicate stronger perceptions of the United States as a nation that is tight and abides by strict social norms. Group differences in cultural tightness were assessed via a two-sample t-test. Furthermore, when participants' cultural tightness scores were entered in the mixed-effects models to predict regional brain activation associated with emotion, the scores were grand-mean centered.

fMRI Data Acquisition, Preprocessing, and Analysis

Brain imaging data were collected using a 3T-Siemens PRISMA MRI scanner. Structural image acquisition included a T1*-magnetization-prepared rapid-acquisition gradient-echo (slice thickness = 0.8 mm; 208 slices; repetition time (TR) = 2400 ms; echo time (TE) = 2.22 ms; matrix = 320 x 320; field of view (FOV) = 256 mm; voxel size = 0.8 x 0.8 x 0.8 mm³; sagittal plane) and a T2*-weighted, matched-bandwidth, high resolution, anatomical scan (slice thickness = 3 mm; 38 slices; TR = 5700 ms; TE = 65 ms; matrix = 192 x 192; FOV = 230 mm; voxel size = 1.2 x 1.2 x 3.0 mm³). Functional image acquisition included collection of T2*-weighted echo-planar images (37 slices; slice thickness = 3 mm; TR = 2000 ms; TE = 25 ms; matrix = 92 x 92; FOV = 230 mm; voxel size = 2.5 x 2.5 x 3.0 mm³).

Preprocessing was carried out using SPM12 (UCL, London, UK), implemented in MATLAB 2018a (Math Works, MA). Volumes were slice-time corrected, realigned to the mean volume to correct for head motion, normalized, warped into the standard stereotactic space defined by the Montreal Neurological Institute (MNI, 2 mm), and smoothed with an 8 mm Gaussian kernel, full width at half maximum to increase signal-to-noise ratios in the functional images. Low-frequency drift across the time series was removed using a high-pass temporal filter with a 128s cutoff.

The fMRI task was modeled using an event-related design with condition duration corresponding to stimulus presentation of fear, neutral, and sad events. Fixed-effects models included a general linear model (GLM) in SPM12 for each of the following conditions at the individual subject level: nonsocial fear, social fear, nonsocial neutral, social neutral, nonsocial sadness, and social sadness. The main effects

were model relative to the null events consisting of the jittered ISIs. The ISIs were not explicitly modeled and therefore constituted an implicit baseline. Random-effect analyses were conducted by submitting the individual subject models to the second level for group analyses. Note that since our primary interest was regional brain activation in regions that have shown consistent differences in emotion and cross-cultural differences during social cognitive and affective processing, here we report analyses of said regions only.

ROI Selection and Analysis

Our primary outcome of interest was activity observed in the 8 ROIs listed in Table 3.1. These regions have consistently shown activation in meta-analyses of emotion (Kober et al., 2008; Lindquist et al., 2012; Vytal & Hamann, 2010) and have demonstrated consistent cross-cultural differences during social-cognitive and social-affective fMRI tasks (Han & Ma, 2014; Shkurko, 2020).

From these 8 ROIs, 6 are cortical regions that we selected based on Han and Ma's (2014) meta-analysis. Specifically, the peak MNI coordinates and spatial extent of these regions, as reported in the meta-analysis, were used to identify corresponding functional regions from the Schaefer atlas (Schaefer et al., 2018). We employed the Schaefer atlas to determine functional regions that not only covered the spatial extent of the selected cortical ROIs but were also centered at the peak coordinates reported in Han and Ma's meta-analysis. We opted for the Schaefer atlas due to its ability to provide more homogenous and neurobiologically meaningful features of brain organization compared to previous parcellations (Schaefer et al., 2018). The Schaefer atlas is based on a multiresolution parcellation derived from both task-fMRI and resting-state fMRI data, encompassing diverse acquisition protocols. As a result, the atlas contains parcels of voxels within resting state intrinsic networks, defined by both structural and functional connections (Schaefer et al., 2018). The publicly available parcellations can be accessed at: https://github.com/ThomasYeoLab/CBIG/tree/master/stable_projects/brain_parcellation/Schaefer2018_LoCalGlobal.

In addition to the 6 cortical ROIs, we included 2 subcortical ROIs: bilateral amygdala. We selected these subcortical regions from our meta-analysis on the brain basis of emotion (Lindquist et al., 2012). Here, we chose peak coordinates in the neural reference space for discrete emotion to represent the amygdala ROIs (see Lindquist et al., 2012, Table S3). The inclusion of the amygdala was based not

only on its relevance to emotion, but also to social cognition (e.g., see Adolphs, 2010) and cultural neuroscience (e.g., see Kwon et al., 2021).

Next, mean parameter estimates were extracted at the specified ROIs for each condition of interest that was modeled at the whole-brain group-level: nonsocial fear, social fear, nonsocial neutral, social neutral, nonsocial sadness, and social sadness. Once extracted, parameter estimates for the conditions of interest were converted from wide to long form to create the outcome of interest, resulting in an “ROI” factor with eight levels. Parameter estimates for the conditions of interest were analyzed in a multilevel framework with regional brain responses nested within participant ($k_1 = 45$) and ROI ($k_2 = 360$). Participants and ROIs were selected as the clustering units since neural responses were made at these levels.

Behavioral Results

Manipulation Check: Self-reported Emotion

Analyses revealed that participants’ in-scanner emotional responses were significantly greater during social events compared to nonsocial events ($b = 0.28$, 95% CI[0.15, 0.41], $SE = 0.07$, $z = 4.20$ $p < .001$), and significantly greater during emotional events compared to neutral events (sadness vs. neutral: $b = 2.08$, 95% CI[1.88, 2.27], $SE = 0.08$, $z = 25.32$, $p < .001$; fear vs. neutral: $b = 1.92$, 95% CI[1.73, 2.12], $SE = 0.08$, $z = 23.46$, $p < .001$; fear vs. sadness, $b = 0.15$, 95% CI[-0.04, 0.34], $SE = 0.08$, $z = 1.85$, $p = .152$). Unexpectedly, we observed a significant interaction between emotion and culture (i.e., participants’ self-reported cultural identities) ($F_{(2, 7755)} = 6.87$, $p = .001$). Post-hoc pairwise comparisons revealed that White American participants’ emotional responses were significantly greater during sad events than fear events ($b = 0.20$, 95% CI[0.01, 0.40], $SE = 0.09$, $z = 2.29$, $p = .058$), whereas Chinese Asian participants’ emotional responses showed no difference between sad and fear events ($b = 0.11$, 95% CI[-0.09, 0.31], $SE = 0.09$, $z = 1.25$, $p = .425$).

These findings, along with a substantial body of prior research using similar evocative stimuli, serve as a concept proof that we successfully induced emotional experiences in participants.

Manipulation Check: Perceptions of Cultural Tightness

As expected, Chinese Asian participants reported that US social norms were significantly looser ($M = 4.57$, $SD = 0.64$) than White American participants ($M = 5.74$, $SD = 1.29$), $t_{(43)} = -3.90$, $p < .001$.

These findings are consistent with evidence that China has relatively tight social norms compared to the United States (e.g., Gelfand et al., 2011). Relative to their home nation, Chinese Asian participants were thus more likely to perceive that the United States is a nation that is loose and tolerates deviance from social norms.

ROI Results

Effects Associated With Emotional Events

Analyses revealed a significant interaction between emotion and ROI ($F_{(14, 1720)} = 6.88, p < .001$), albeit this two-way interaction was qualified by a three-way interaction between emotion, ROI, and culture, which we explicate in the section *Effects Associated with Cultural Context*. Nonetheless, as predicted, the two-way interaction between emotion and ROI revealed significantly greater activation in regions consistently associated with emotional experiences—MPFC/dACC, valINS, AMY, TP, and TPJ—for fear and sad events compared to neutral events.

In Table 3.2, we list the results of this two-way interaction by region regardless of significance. The results reflect regional brain activation associated with the emotional events relative to neutral events. With respect to regional brain activation between the two emotional events, fear and sad, there were no clear differences beyond the findings that sad events recruited significantly greater activation in bilateral amygdala than fear events (left: $b = 0.10, 95\% \text{ CI}[0.02, 0.18], SE = 0.03, t = 2.92, p = .010$; right: $b = 0.13, 95\% \text{ CI}[0.05, 0.47], SE = 0.03, t = 3.73, p < .001$), and fear events recruited significantly greater activation in the TPJ than sad events ($b = 0.12, 95\% \text{ CI}[0.04, 0.20], SE = 0.03, t = 3.59, p = .001$).

Effects Associated with Social Events

Analyses revealed a significant interaction between situation and ROI ($F_{(7, 1720)} = 12.16, p < .001$). As predicted, the interaction demonstrated significantly greater activation in regions implicated in visceromotor activation, abstract reasoning, and social cognition—MPFC/dACC, AMY, DMPFC, TP, and TPJ—for social events compared to nonsocial events. Table 3.2 lists these results by region regardless of significance.

Effects Associated with Cultural Context

With respect to cultural identity, we found, as mentioned, a significant three-way interaction between emotion, culture, and ROI ($F_{(14, 1720)} = 2.48, p = .002$). This three-way interaction revealed

greater activation in regions implicated in social cognition (TP, TPJ) during emotional events compared to neutral events for Chinese Asian participants but not White American participants, and greater activation in regions implicated in visceromotor activation (vAINS) and self-referencing (MPFC/dACC) during emotional events compared to neutral events for White American participants but not Chinese Asian participants. Moreover, while both Chinese Asian participants and White American participants showed increased activation in bilateral amygdala during sad events compared to neutral events, the difference between the conditions was significantly greater among White American participants compared to Chinese Asian participants (left: $b = 0.27$, $SE = 0.07$, 95%CI[0.11, 0.42], $t = 3.91$, $p < 0.001$; right: $b = 0.21$, $SE = 0.07$, 95%CI[0.06, 0.37], $t = 3.17$, $p = 0.004$). See Figure 3.2 for a bar-plot illustration of these results.

With respect to perceptions of cultural tightness, analyses revealed a significant three-way interaction between participants' perceptions of US cultural tightness, culture (i.e., cultural identity), and ROI ($F_{(7, 287)} = 2.84$, $p = .007$). This three-way interaction indicated that Chinese Asian participants who perceived greater cultural tightness in the United States also showed greater activation in regions implicated in executive control (DLPFC) and self-referential processing (DMPFC) during emotion experience, whereas White American participants did not show this trend (see Figure 3.3).

Table 3.2: Regional Brain Activation Moderated by Emotional and Situational Events

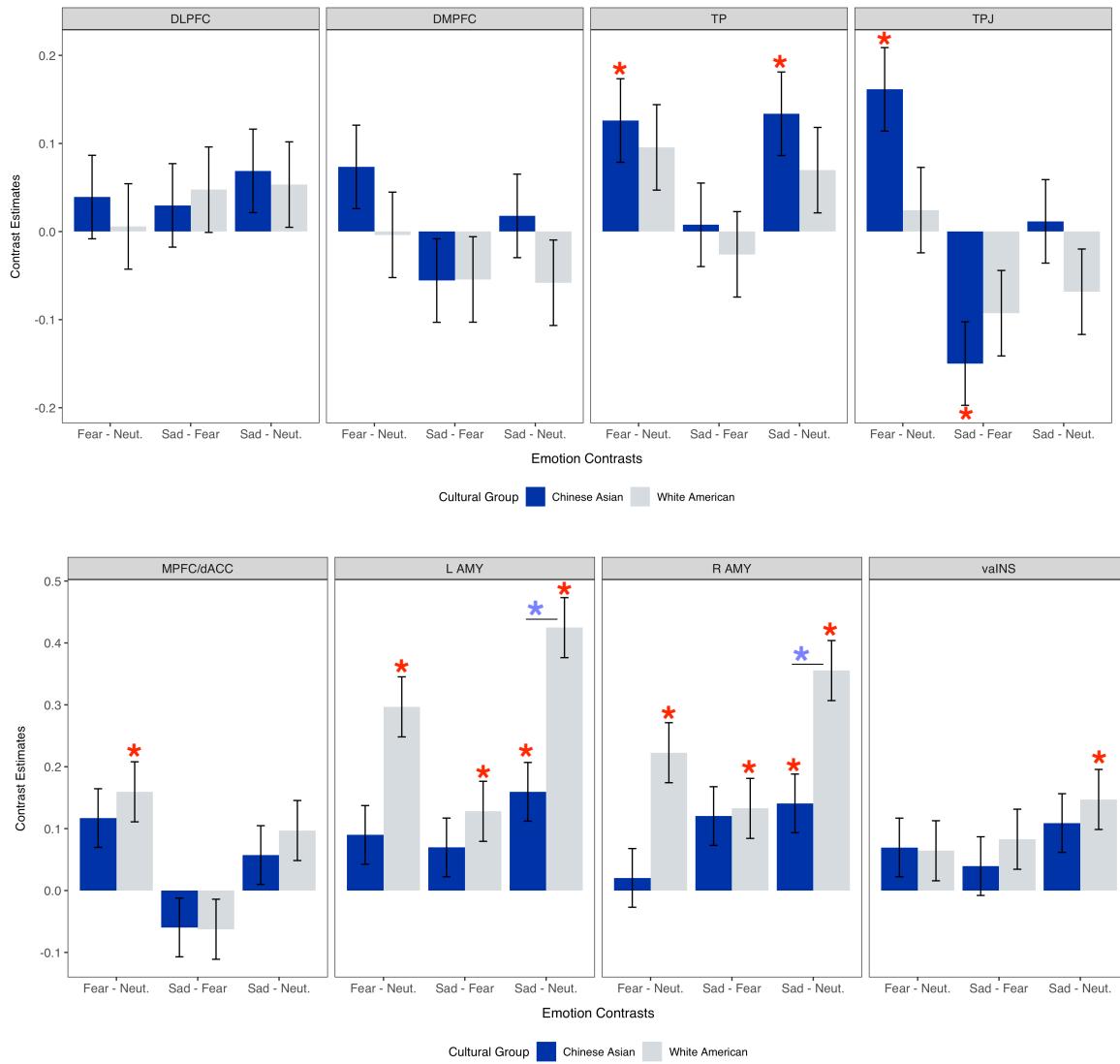
Effect	ROI	Estimate	SE	df	95% CI	t	p
Fear > Neutral	MPFC/dACC	0.14	0.03	1720	[0.06, 0.22]	4.08	< .001
	AMY (L)	0.19	0.03	1720	[0.11, 0.27]	5.70	< .001
	AMY (R)	0.12	0.03	1720	[0.04, 0.20]	3.59	.001
	DLPFC	0.02	0.03	1720	[-0.06, 0.10]	0.66	.785
	DMPFC	0.03	0.03	1720	[-0.04, 0.11]	1.03	.560
	TP	0.11	0.03	1720	[0.03, 0.19]	3.27	.003
	TPJ	0.09	0.03	1720	[0.01, 0.17]	2.74	.017
	valNS	0.07	0.03	1720	[-0.01, 0.15]	1.97	.119
	Sad > Neutral	MPFC/dACC	0.08	0.03	1720	[-0.00, 0.16]	2.28
Sad > Neutral	AMY (L)	0.29	0.03	1720	[0.21, 0.37]	8.62	< .001
	AMY (R)	0.25	0.03	1720	[0.17, 0.33]	7.32	< .001
	DLPFC	0.06	0.03	1720	[-0.02, 0.14]	1.80	.169
	DMPFC	-0.02	0.03	1720	[-0.10, 0.06]	-0.59	.823
	TP	0.10	0.03	1720	[0.02, 0.18]	3.00	.008
	TPJ	-0.03	0.03	1720	[-0.11, 0.05]	-0.84	.680
	valNS	0.13	0.03	1720	[0.05, 0.21]	3.78	< .001

Table 3.2 cont.

Effect	ROI	Estimate	SE	df	95% CI	t	p
Social > Nonsocial	MPFC/dACC	0.07	0.03	1720	[0.02, 0.13]	2.63	.009
	AMY (L)	0.15	0.03	1720	[0.09, 0.20]	5.34	< .001
	AMY (R)	0.24	0.03	1720	[0.19, 0.30]	8.73	< .001
	DLPFC	0.00	0.03	1720	[-0.06, 0.05]	-0.05	.962
	DMPFC	0.07	0.03	1720	[0.01, 0.12]	2.47	.014
	TP	0.14	0.03	1720	[0.09, 0.20]	5.24	< .001
	TPJ	0.22	0.03	1720	[0.17, 0.28]	8.12	< .001
	valNS	0.01	0.03	1720	[-0.04, 0.06]	0.34	.732

Note. Regions of interest (ROIs) are: Anterior cingulate cortex (ACC), amygdala (AMY), dorsomedial prefrontal cortex (DMPFC), temporal pole (TP), temporoparietal junction (TPJ), and ventral anterior insula (valNS). L/R = in either the left (L) or right (R) cerebral hemisphere.

Figure 3.2: Regional Brain Activity Comparisons by Emotion and Culture



Note. Presented here are estimates derived from pairwise comparisons of the emotional events (e.g., Fear – Neutral) by ROI and cultural group, and corrected for multiple comparisons. Red asterisks denote a significant difference from zero, whereas lavender asterisks denote a significant difference between the cultural groups; the amygdala was the only ROI that survived this significance thresholding.

Figure 3.3: Scatterplot of Perceptions of Cultural Tightness and Regional Brain Activation

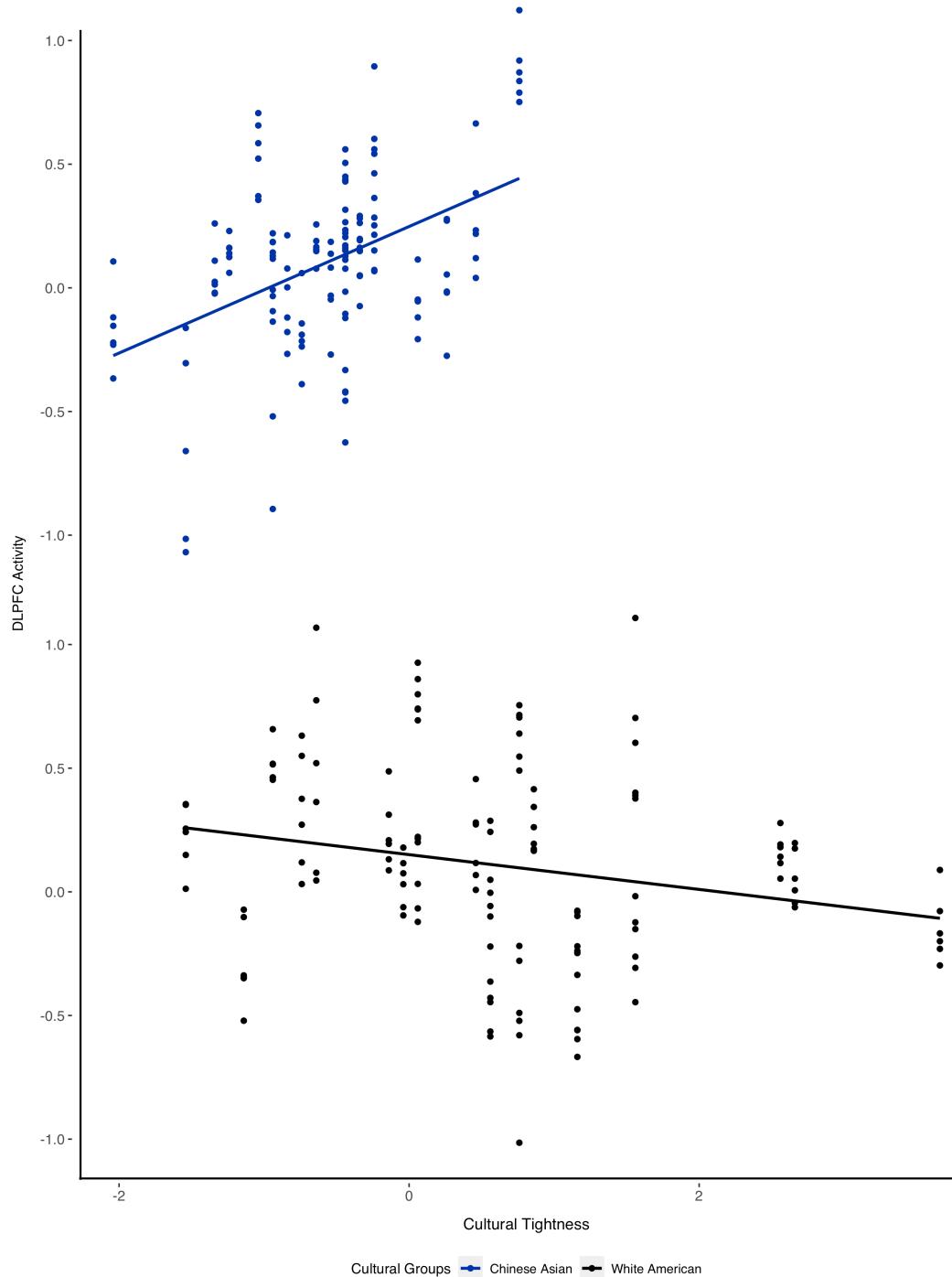
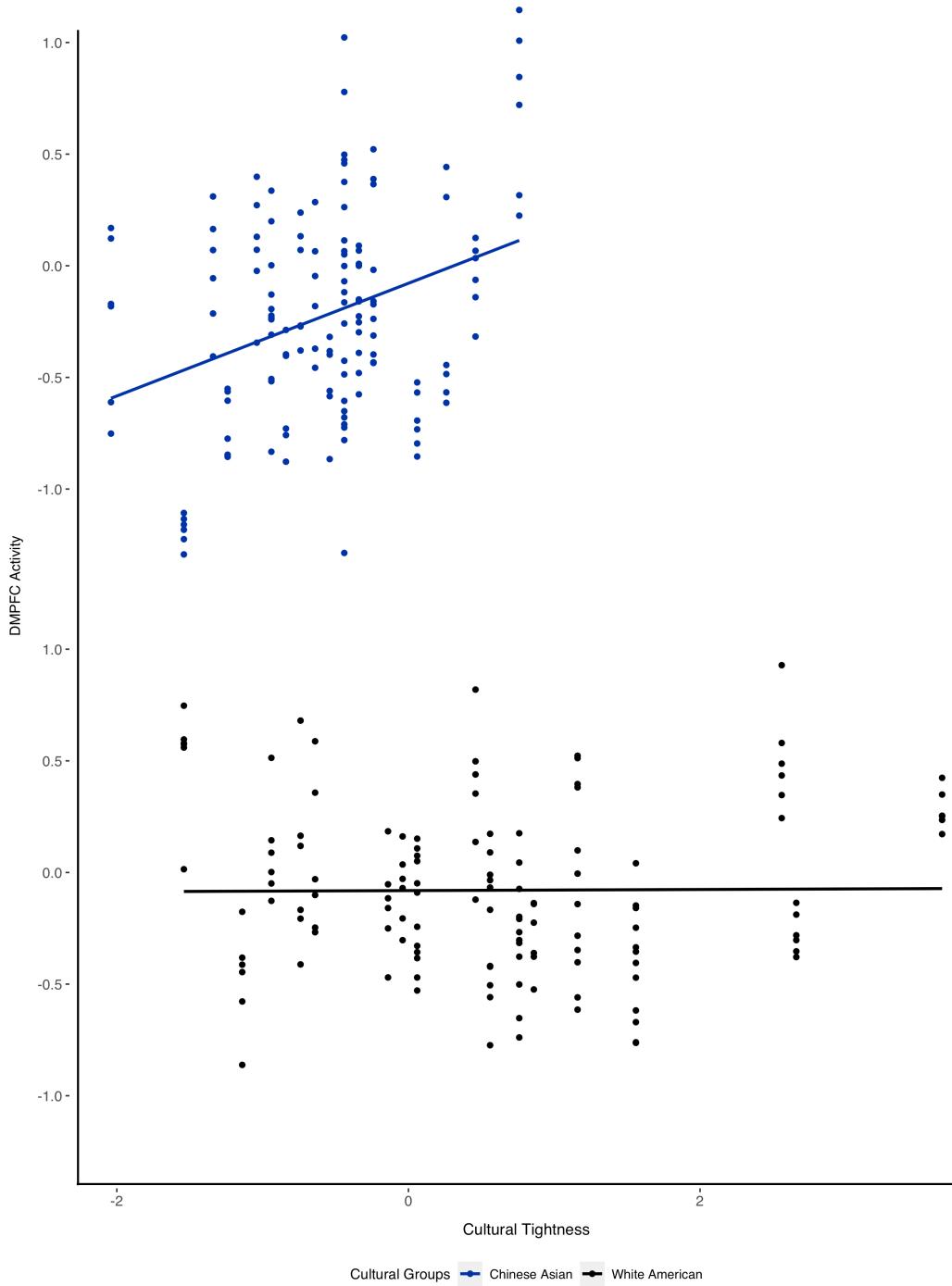


Figure 3.3 cont.



Note. The six data points per participant reflect the six situated events in the fMRI experiment, that is, the combined events of emotion (fear, neutral, sad) and situation (social, nonsocial) conditions.

Discussion

Here we explored how situational and cultural contexts shape the brain basis of emotion. Our theoretical framework proposes that even instances of the same emotion category have behavioral, physiological, cognitive, and subjective qualities that vary across different situational and cultural contexts (Barrett, 2014; Lindquist, 2013; Mesquita & Boiger, 2014; see also Brosch & Sander, 2013; Larsen et al., 2017; Lebois et al., 2020; Scherer & Moors, 2019). We hypothesized that the brain basis of emotions reflects this situatedness. Our findings provide support for this hypothesis, suggesting that brain activity associated with emotions differs depending on the social and cultural contexts in which those emotions are experienced. We argue that these contextual factors should not be overlooked in affective neuroscience studies, which often seek to identify brain regions that show invariant activity associated with specific emotions across all contexts (e.g., see Lindquist et al., 2012 for a discussion).

Emotion in Social Contexts

Social contexts have a significant impact on people's emotions. Compared to nonsocial contexts, social contexts can intensify subjective experience, pressure people to feel certain ways, influence whether emotions should be affiliative or regulated, and impact the way emotions manifest in relationships (Bastian et al., 2012, 2017; Boiger & Mesquita, 2012; Clark et al., 2017; De Leersnyder et al., 2018; Peters & Kashima, 2007; Sels et al., 2017). It is therefore not surprising that Chinese Asian and White American participants in our study reported feeling more intensely emotional in the social, relative to nonsocial, conditions of fear and sadness.

For example, experiencing sadness in reaction to others may create affordances that can intensify subjective experience, such as inferring others' mental states, anticipating interpersonal behaviors, or increasing awareness of oneself or the environment (Haas et al., 2015; Kassam & Mendes, 2013; Lin et al., 2018b; McDonald et al., 2020; Satpute et al., 2013; Stanley, 2016). Our results suggest that these context-dependent affordances also contribute brain activity associated with emotion. During the social conditions of fear and sadness, both Chinese Asian and White American participants showed significantly greater activation in regions associated with visceromotor activation and emotional vigilance such as MPFC/dACC and AMY. In addition, both Chinese Asian and White American participants showed significantly greater activation in regions associated with representing one's own internal state and

monitoring the behavior of others such as DMPFC, TP, and TPJ. These findings are consistent with theoretical models of emotion in which emotions are highly tuned to the context, and suggest that the social context in which an emotion occurs is linked to its neurophysiological manifestation (Atzil et al., 2023; Barrett, 2006, 2022; Lindquist et al., 2022; Mesquita et al., 2017).

In contrast, none of the ROIs examined showed greater activation for nonsocial versus social contexts, perhaps because we focused on ROIs related to visceromotor activation, abstract representation, and mentalizing, and did not include regions associated with spatial processing or motor control. Nonetheless, our findings underscore the importance of considering situational context when investigating the neural basis of emotion, as it can significantly shape the subjective experience and neural representation of emotions.

Emotion in Cultural Contexts

Much of the fMRI literature on emotion and culture focuses on neural differences in emotion perception from faces or social cognition between cultural groups (see Shkurko, 2020, for a review). This study advances the cultural affective neuroscience literature by demonstrating that the neural representation of induced emotional experiences differs, in part, because of the cultural context in which emotion knowledge was enculturated. Specifically, we tested a set of brain regions that have been found to show cultural differences in social and affective processes. We replicated much of Han and Ma's (2014) findings, showing that Chinese Asian participants primarily exhibited greater activation in regions implicated in abstract representation and social-cognitive processing (TP and TPJ) during emotion. These results align with previous behavioral evidence suggesting that East Asians participants are more likely to show greater mentalizing and perspective-taking than Westerners participants.

In contrast, White American participants primarily showed greater activation in regions implicated in visceromotor activation (AMY and valNS) during emotion. Both AMY and valNS form part of a brain network that correlates with the intensity of affective experiences (Touroutoglou et al., 2012) and sympathetic arousal (Kleckner et al., 2017). These findings are consistent with evidence that East Asians prioritize lower-arousal emotions and in fact do experience less arousal during emotions than Westerners (Chentsova-Dutton & Tsai, 2010; Heine, Kitayama, Lehman, et al., 2001; Heine, Kitayama, & Lehman, 2001; Y. Ma et al., 2014; Sui et al., 2009; Tsai et al., 2007).

Our study also examined how individual differences in perceptions of US social norms interacted with participants' cultural background to predict differences in brain activity during emotion experience. We found that the more that Chinese Asian participants perceived that the United States had tight cultural norms, the more they showed activation in regions implicated in executive control (DLPFC) and self-referential processing (DMPFC) across emotional experiences. In contrast, variation in White American's perceptions of cultural tightness for the United States did not predict differential activation in these brain regions. Although speculative, these findings may suggest that those Chinese participants who perceive US cultural norms to be tighter may be engaging in greater attention to the context and other-focused awareness across emotional situations. These findings highlight the importance of considering the role of individual differences in cultural perception and their interaction with cultural background in shaping neural responses to emotion.

Limitations

Our study has several limitations worth noting. First, while images are commonly used to elicit emotions in fMRI studies, they may not capture the full range of emotional experiences that people have in daily life. Additionally, the image set used in our study was normed in a US sample, which may limit the generalizability of our findings to other cultures. Nonetheless, previous research suggests that the emotional valence of the images we used is similar across cultures, including Chinese Asian participants (e.g., Gong & Wang, 2016; Qu & Telzer, 2017).

Second, although the mere presence of other humans certainly implies the presence of social context (Cao et al., 2014), there are multiple dimensions on which social contexts differ (Fan et al., 2021). It bears note that cultural contexts also vary in multiple dimensions: Culture is itself a multi-faceted construct and it would be interesting to examine how other aspects of culture impact brain activity related to emotion experience, particularly in a developmental framework (e.g., see Qu et al., 2021). Indeed, as mentioned in the introduction, we chose to recruit participants from mainland China and the United States because the East-West paradigm has been a productive model for testing cultural differences in behavior and brain function. However, two-culture comparisons have important limitations (Vignoles et al., 2016; see also Denkhaus & Bös, 2012) and emotions vary across the globe (Jackson et al., 2019). Furthermore, we chose to recruit a racially and ethnically homogenous sample of US Americans to match

the relative racial and ethnic homogeneity in mainland China, which comes with its own limitations. There is, of course, important variation in culture within the United States (e.g., Cohen et al., 1996; Niedenthal et al., 2019; Senft et al., 2021; Wood et al., 2023) that should be modeled in future work.

Third, there were limitations associated with our sample. Our sample was small compared to current standards for neuroimaging. However, our sample size is commensurate with many cultural neuroscience studies, which typically involve similar or even smaller sample sizes (e.g., Adams et al., 2010; Cheon et al., 2011; de Greck et al., 2012; Freeman et al., 2009; Immordino-Yang et al., 2014; Park et al., 2017; Qu & Telzer, 2017). Concerns about the sample size are somewhat offset by the fact that we based our hypotheses off of findings replicated and supported through comprehensive quantitative and qualitative reviews of the literature (Han & Ma, 2014; Shkurko, 2020). Indeed, our findings replicate activation in regions of interest shown to be associated with cultural differences in affective responding in the past (Han & Ma, 2014; Shkurko, 2020). Nonetheless, our sample is small in part because it was difficult to recruit and retain Chinese Asian participants to partake in this study of emotion and more Chinese Asian participants did not complete the entirety of the scanning tasks.

Furthermore, our sample of Chinese Asian participants living in the United States—and especially those who consented to participate and who completed our study—may underestimate the degree of cultural differences that exist in brain activity associated with emotion experience. Indeed, previous work suggests that individuals who voluntarily move to a different country or culture may *a priori* resemble members of the new, host culture on certain psychological dimensions (Feng et al., 2017). Yet our examination of individual differences in perceptions of social norms in the United States provides some insight into the cultural factors that influence neural responses to emotional events. Specifically, we were able to examine individual differences in perceptions of cultural tightness in the United States, which predicted Chinese Asian—but not White American—participants' neural responses in the DMPFC and DLPFC. Those Chinese Asian participants who perceived the United States to have quite tight cultural norms presented a neural profile that is consistent with what individuals from prototypically “collectivist” cultures might be expected to show (e.g., see de Greck et al., 2012); that is, Chinese Asian participants in the present study showed greater activation in brain regions associated with attention and behavior regulation and the representation of others' mental states during emotion. It is interesting that this was the

case in our task, even when there was no explicit goal to regulate one's emotions (e.g., see Davis et al., 2012). We are unsure, however, why some individuals from mainland China perceived the United States to have tighter cultural norms. One hypothesis is that these individuals may have been less acculturated to their host nation than those Chinese Asian individuals who perceived the United States to have looser social norms. Alternatively, those who perceived tighter cultural norms might have selected to move to the United States for different reasons than those who perceived it to have looser social norms (e.g., exclusively to pursue educational opportunities v. because they wished to live in a nation with looser norms). Future research should explicitly examine the impact of emotional acculturation on brain activation (as in behavioral studies; e.g., De Leersnyder et al., 2011) and more generally unpack individual differences within culture that could drive brain activity.

Lastly, the present study examined task-related brain activation using univariate analyses. These types of analyses are still the norm in neuroimaging studies, but research is increasingly examining the extent to which brain regions function together as networks. Future research will examine differences in functional connectivity in brain regions associated with emotion (e.g., an allostatic interoceptive network; Kleckner et al., 2017) across forms of context.

Conclusion

Here we investigated the role of social and cultural contexts in shaping the brain basis of emotion. Our findings provide evidence that the brain basis of emotion varies depending on the social and cultural context in which emotions are experienced. Emotions are increasingly recognized as being highly context-dependent, and it is essential for future research to explore how emotion categories and various forms of context interact to shape the neural responses associated with emotions. Furthermore, incorporating more diverse samples in basic models of emotion is crucial to gaining a comprehensive understanding of how the human brain creates emotions. The field of human neuroscience is no longer in its infancy, but it is certainly not mature. Our study highlights the need for continued research on how social and cultural contexts influence the brain basis of emotion.

CHAPTER 4: DIRECTED FUNCTIONAL CONNECTIVITY AND SUB-GROUPING DURING EMOTION

Introduction

Constructionist theories of emotion advocate for empirical investigations into whether diverse neural mechanisms can underpin the same emotion category (Barrett & Satpute, 2019). The idea that multiple mechanisms can achieve the same result is known as *degeneracy*, and complex systems that adapt to their environments, such as biological systems, demonstrate degeneracy (Edelman & Gally, 2001; Marder & Taylor, 2011; Sporns et al., 2000; Tononi et al., 1999; Whitacre & Bender, 2010; see also Charbonneau et al., 2022). Growing evidence is suggestive of the hypothesis that degenerate neural network patterns are associated with the same emotion category. For example, fMRI studies provide evidence for the role of several large-scale networks in giving rise to the same emotional state (e.g., see Doyle et al., 2022; Wager et al., 2015; Wilson-Mendenhall et al., 2013a), and identical twin studies involving amygdala lesions provide support for the existence of multiple neural pathways for fear. For example, despite monozygotic twins having bilateral lesions to the amygdala and identical genetics, one twin typically shows normal fear processing while the other does not (e.g., Becker et al., 2012). Such findings, among others (e.g., Koide-Majima et al., 2020), illustrate the constructionist thesis that there is meaningful diversity in the neural mechanisms for an emotion category such as fear.

Relevant to the present dissertation is a study that revealed evidence of degeneracy in patterns of directed functional connectivity underlying states of anger and anxiety (Doyle et al., 2022). In this study, participants self-generated experiences of anger and anxiety in response to unpleasant music while undergoing 5 min fMRI blocks. Doyle et al. (2022) then used the Group Iterative Multiple Model Estimation (GIMME) subgrouping procedure, a data-driven search algorithm that utilizes both individual and group-level information to derive directed functional connectivity maps (Gates & Molenaar, 2012), to identify the presence of statistically differentiable patterns of connectivity between large-scale brain networks associated with the emotion induction conditions. The subgrouping procedure, known as subgrouping GIMME (S-GIMME), determines subgroup assignments in an unsupervised manner by

analyzing individuals' connectivity maps and performing community detection to identify subgroups with similar connectivity patterns (Gates et al., 2017). Doyle et al. (2022) specifically examined whether there were differences in connectivity patterns between large-scale brain networks, such as the default mode network, salience network, visual networks, and attention networks, each consisting of multiple regions of interest (ROIs) (using a network-based parcellation from Shirer et al., 2012).

Using s-GIMME, Doyle et al. (2022) first entered time-series data from each condition (anger, anxiety) into an unsupervised analysis. This analysis revealed consistent patterns of activation associated with the experimental emotion induction conditions. One subgroup consisted of relatively more anger scans (64% anger scans), and another consisted of relatively more anxiety scans (82% anxiety) (a third subgroup had a roughly 50%-50% mix of both). Doyle et al (2022) then used S-GIMME to examine whether there were statistically differentiable subgroups *within* each emotion induction condition. S-GIMME did indeed identify meaningful variability in the functional connectivity patterns associated with experiences of anger and anxiety. Within both the anger and anxiety conditions, s-GIMME revealed two major subgroups of participants whose connectivity patterns differed significantly. In both cases, participants' self-reported intensity of the induced emotion category did not differ between the subgroups. For instance, participants in both anger subgroups self-reported equivalent levels of anger, and their anger experiences were equivalent in valence and arousal (Doyle et al., 2022). These findings suggest that there is degeneracy (i.e., different neural pathways) for the same emotional experience (operationalized as similarity in the intensity of the felt emotion category and the valenced and arousing features of that category).

One might also expect cultural contexts to contribute to the development of meaningful variability in the functional connectivity patterns associated with emotion experience. The human brain's wiring is heavily influenced by the immediate ecological environment in which it develops (Atzil & Barrett, 2017; Atzil & Gendron, 2017), which varies across cultures (Chiao, 2018; Gendron et al., 2020; Lindquist et al., 2022; see also Qu et al., 2021). Thus, Study 3 of the dissertation aims to investigate whether underlying directed functional connectivity associated with emotion depends on cultural and situational contexts, and whether different patterns of directed functional connectivity underlie the same emotional experiences of fear and sadness.

Study 3 extends Study 2 in at least two ways. First, building on newer network neuroscience models of emotion (Barrett & Satpute, 2013; Leshin & Lindquist, 2020; Lindquist & Barrett, 2012; Pessoa, 2023; Wager et al., 2015), Study 3 examines patterns of directed functional connectivity that are situated in specific situational and cultural contexts. Second, Study 3 uses GIMME to investigate, via both confirmatory and data-driven procedures, the factors that best explain connectivity maps associated with emotion. Specifically, Study 3 first uses confirmatory subgrouping GIMME to examine whether directed functional connectivity associated with emotional experience varies by the situational (social v. nonsocial), cultural (White American participant v. Chinese Asian participant), or emotional context (fear v sadness), or a combination of these contexts. Study 3 then uses the unsupervised procedure in GIMME (S-GIMME) to examine which factors under study (emotion, situation, culture, or other non-manipulated factors such as gender) predict data-driven identified subgroups of directed functional connectivity.

As in Study 2, Study 3 uses ROIs that have consistently shown activation in meta-analyses of emotion (Kober et al., 2008; Lindquist et al., 2012; Vytal & Hamann, 2010) and have consistently demonstrated cross-cultural differences during social-cognitive and social-affective processing (Han & Ma, 2014; Shkurko, 2020). Please see Table 4.1 for a list of the a priori ROIs.

Table 4.1: Study 3 Neural Regions

Region	ROI Abbr.	Hemisphere
Amygdala	AMY	Left
Amygdala	AMY	Right
Dorsal anterior insula	daINS	Right
Dorsolateral prefrontal cortex	DLPFC	Left
Dorsomedial prefrontal cortex	DMPFC	Right
Fusiform	FS	Left
Fusiform	FS	Right
Medial prefrontal extending into anterior cingulate	MPFC/dACC	Left
Medial orbital frontal cortex	MOFC	Right
Temporoparietal junction	TPJ	Right
Temporal Pole	TP	Right
Ventral anterior insula	vaINS	Left
Ventral lateral prefrontal cortex	VLPFC	Right

Methods

Participants

Participants were the 45 participants for whom we had complete data from Study 2. Specifically, there were 23 Chinese Asian participants ($M_{age} = 20.8 \pm 2.4$) of whom 12 self-identified as female and 11 as male and 22 White American participants ($M_{age} = 21.9 \pm 3.1$) of whom 11 self-identified as female and 11 as male. Chinese Asian participants were born in provinces of mainland China and raised by monolingual Mandarin-speaking Chinese-born parents, and all denied ever residing outside their provinces prior to arriving to the United States as adults. Note that we excluded Chinese Asian participants raised in Hong Kong, Macau, or Taiwan before arriving in the United States, as these regions have had relatively more exposure to Western norms due to their histories of colonization (e.g., see L. Li et al., 2020; Qu et al., 2020). In contrast, White American participants were born and raised in the United States by primarily monolingual English-speaking non-Hispanic White American-born parents, and all denied every residing outside of the United States. Male participants were on average 1.6 years older than female participants ($F_{(1, 41)} = 3.92, p = .054$). No further age differences were observed.

Because Chinese Asian participants had lived in the United States for less than 24 months ($M = 20.8 \pm 15.1$), we used the Test of English as a Foreign Language (TOEFL; Educational Testing Service) ($M = 107.2 \pm 4.5$) to confirm proficiency in spoken and written English. There was no difference in time spent in the United States ($p = .65$) or in TOEFL scores ($p = .12$) between sexes for Chinese Asian participants.

Task and Stimuli

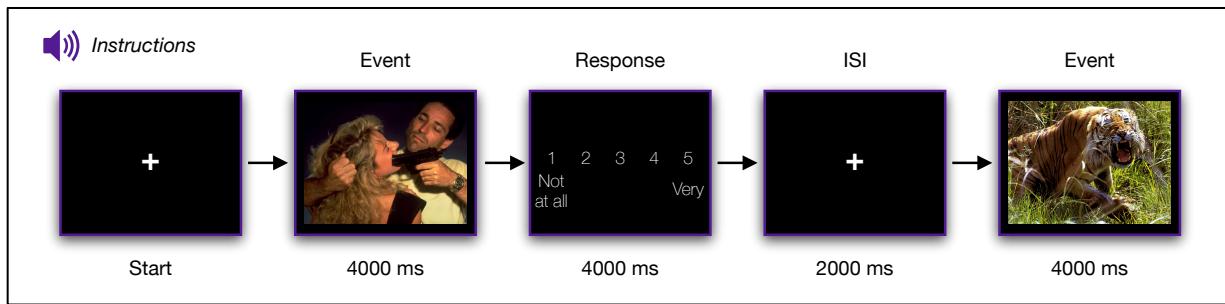
Stimuli from the IAPS and related data sets were used to induce fear, neutral affect, and sadness. One hundred and eighty images were used in the fMRI experiment, resulting in 180 trials or events. Half of these events depicted humans (social context; $n = 90$) and half depicted content devoid of humans (nonsocial context; $n = 90$). Each set of the situational contexts—social and nonsocial—included fear ($n = 30$), neutral ($n = 30$), and sad ($n = 30$) events. The fMRI experiment comprised five experimental runs.

Per our prior work using electroencephalogram (Pugh, Choo, et al., 2022; Pugh, Huang, et al., 2022), each trial began with a stimulus presentation—fear, sad, or neutral—that lasted 4000 ms. This stimulus event was followed immediately by a response scale whose duration was also 4000 ms. During

the response scale, participants used a 5-point Likert-type scale to report their degree of felt intensity in response to the preceding fearful, sad, or neutral event. Participants made these responses using a button box in their right hand. Participants were instructed outside the scanner, and reminded at the beginning of every experimental run, that a value of 1 on the scale (“not at all”) denoted low-to-no reactivity in response to fear, sad, or neutral events, whereas a value of 5 on the scale (“very”) denoted high, intense reactivity in response to fear, sad, or neutral events. Immediately following the response scale was an interstimulus interval (ISI) presentation ($M_{ISI} = 2000$ ms). Please see Figure 4.1 for an illustration of an fMRI trial.

To evoke contextual effects from still images (see Aldao, 2013; Wilson-Mendenhall et al., 2013b for discussions), participants were instructed to imagine experiencing the depicted events from a first-person perspective, as if watching the events unfold before them. Participants were instructed to pay particular attention to their subjective experience of the events, and to use that information to answer the response scales. Participants engaged with the task on a laptop computer during a practice run before entering the scanner. The design of the practice run was identical to the fMRI task but consisted of only one run and exposed participants to disgust and neutral stimuli that varied in sociality. Participants verified they understood the task by explicitly providing reactions to the practice stimuli that were unequivocally related to the depicted events, self-focused, and encapsulated in a value between 1 (low-to-no reactivity) and 5 (high, intense reactivity).

Figure 4.1: fMRI Trial



Note. Participants completed five experimental runs at 6 min per run. Instructions for self-immersion and response scales were repeated to participants before the start of each run. The 2×3 within-subjects design of the experiment—Situation (social, nonsocial) \times Emotion (fear, neutral, sad)—yielded “social-fear” trials (e.g., knife-wielding individuals), “nonsocial-fear” trials (e.g., an impending tornado), “social-neutral” trials (e.g., people walking), “nonsocial-neutral” trials (e.g., landscapes), “social-sad” trials (e.g., people attending a funeral), and “nonsocial-sad” trials (e.g., injured animals). The figure above illustrates a complete social-fear trial with the start of a nonsocial-fear trial.

fMRI Data Acquisition, Preprocessing, and Analysis

Brain imaging data were collected using a 3T-Siemens PRISMA MRI scanner. Structural image acquisition included a T1*-magnetization-prepared rapid-acquisition gradient-echo (slice thickness = 0.8 mm; 208 slices; repetition time (TR) = 2400 ms; echo time (TE) = 2.22 ms; matrix = 320 x 320; field of view (FOV) = 256 mm; voxel size = 0.8 x 0.8 x 0.8 mm³; sagittal plane) and a T2*-weighted, matched-bandwidth, high resolution, anatomical scan (slice thickness = 3 mm; 38 slices; TR = 5700 ms; TE = 65 ms; matrix = 192 x 192; FOV = 230 mm; voxel size = 1.2 x 1.2 x 3.0 mm³). Functional image acquisition included collection of T2*-weighted echo-planar images (37 slices; slice thickness = 3 mm; TR = 2000 ms; TE = 25 ms; matrix = 92 x 92; FOV = 230 mm; voxel size = 2.5 x 2.5 x 3.0 mm³).

Preprocessing was carried out using SPM12 (UCL, London, UK), implemented in MATLAB 2018a (Math Works, MA). Volumes were slice-time corrected, realigned to the mean volume to correct for head motion, normalized, warped into the standard stereotactic space defined by the Montreal Neurological Institute (MNI, 2 mm), and smoothed with an 8 mm Gaussian kernel, full width at half maximum to increase signal-to-noise ratios in the functional images. Low-frequency drift across the time-series was

removed using a high-pass temporal filter with a 128s cutoff. In addition to these basic preprocessing steps, we submitted each participants' data to individual-level ICA to remove motion-related signal from the time-series. We then regressed out 8 nuisance regressors from the original time-series: 6 motion parameters generated during realignment and the average signal from both the white matter and cerebrospinal fluid masks. Finally, slices with greater than 2 mm of motion were scrubbed from the time-series to remove the effects of large, sudden movements on the functional data. Previous work (see Ceric et al., 2017) has shown that these strategies reduce the influence of motion on functional connectivity analyses.

ROI Selection and Time-series Extraction

We are interested in directed functional connectivity patterns between the 13 ROIs listed in Table 4.1. These regions have consistently shown activation in meta-analyses of emotion (Kober et al., 2008; Lindquist et al., 2012; Vytal & Hamann, 2010) and have demonstrated consistent cross-cultural differences during social-cognitive and social-affective fMRI tasks (Han & Ma, 2014; Shkurko, 2020). The majority of these regions are cortical regions whose ROI masks for the present study were selected from the Schaeffer atlas (Schaeffer et al., 2018). We used parcellations from the 500-parcel atlas; we selected parcellations that cover MNI coordinates from relevant meta-analyses (i.e., DLPFC, DMPFC, MPFC/dACC, TPJ, TP, and valNS from Han & Ma, 2014; AMY, daINS, FS, MOFC, and VLPFC from Lindquist et al., 2012). We opted for the Schaeffer atlas due to its ability to provide more homogenous and neurobiologically meaningful features of brain organization compared to previous parcellations (Schaefer et al., 2018). The Schaeffer atlas is based on a multiresolution parcellation derived from both task-fMRI and resting-state fMRI data, encompassing diverse acquisition protocols. As a result, the atlas contains parcels of voxels within resting state intrinsic networks, defined by both structural and functional connections (Schaefer et al., 2018). The publicly available parcellations can be accessed at: https://github.com/ThomasYeoLab/CBIG/tree/master/stable_projects/brain_parcellation/Schaefer2018_LocalGlobal.

As for the two subcortical regions, bilateral amygdala, we manually constructed these masks given that the Schaeffer atlas does not provide subcortical masks. We constructed the amygdala ROI

masks using FSLeyes. Specifically, we centered 6 mm spheres at the amygdala coordinates in our meta-analysis on the brain basis of emotion (see Lindquist et al., 2012; Table S3).

Once the parcellations for the ROIs in Table 4.1 were gathered and constructed, we used the CONN toolbox to extract time-series data from the specified ROIs. We entered in CONN a single mask containing all ROIs then used CONN's ROI-to-ROI analysis feature to obtain the average fMRI signal within each ROI for every participant. By default, CONN extracts the entire time-series across all sessions without any condition-specific filtering. We therefore specified condition-specific filters so that time-series data were condition-specific (i.e., 6 conditions reflecting the combination of situation and emotion factors) for each ROI for every participant. The data structure of these files was organized as a matrix, where rows represented the discrete time points (TRs), and columns represented the ROIs listed in Table 4.1. The TRs were specific to the combination of the within-subject factors, emotion (fear, sad; we excluded neutral in these analyses) and situation (social, nonsocial). Therefore, each participant had four separate time-series data files corresponding to Social Fear, Nonsocial Fear, Social Sad, and Nonsocial Sad conditions. Lastly, with the between-subject factor (culture) in mind, eight a priori subgroups were created: Nonsocial Fear for Chinese Asian participants (1), Nonsocial Sadness for Chinese Asian participants (2), Social Fear for Chinese Asian participants (3), Social Sadness for Chinese Asian participants (4), Nonsocial Fear for White American participants (5), Nonsocial Sadness for White American participants (6), Social Fear for White American participants (7), and Social Sadness for White American participants (8). Each time-series file was named using these subgroup labels in preparation for network analyses. This meant that each participant had four time-series data files corresponding to the four evocative conditions.

Group Iterative Multiple Model Estimation (GIMME)

Study 3 uses GIMME to identify directed functional connectivity patterns that may be associated with the experimental conditions. GIMME is a data-driven search algorithm that utilizes both individual and group-level information to derive directed functional connectivity maps (Gates & Molenaar, 2012). GIMME employs unified SEM (Gates et al., 2010; Kim et al., 2007) and extended unified SEM (Gates et al., 2011) to estimate connectivity graphs, assessing whether the presence of a path between regions of interest (ROIs) significantly improves the overall model fit to the time-series data. GIMME estimates both

contemporaneous effects (e.g., ROI₁ at t predicts ROI₂ at t) and lagged effects (e.g., ROI₁ at $t-1$ predicts ROI₂ at t) between ROIs, as well as the autoregressive effect (e.g., ROI₁ at $t-1$ predicts ROI₁ at t) for each ROI time-series. GIMME further evaluates the directional paths by testing if a specific ROI can predict another ROI while accounting for the predicted ROI's autoregressive effect (i.e., establishing Granger Causality) and other possible contemporaneous effects (e.g., ROI₃ predicts ROI₂), including simultaneous reciprocal paths (e.g., ROI₂ predicting ROI₃).

Notably, GIMME diverges from numerous existing functional connectivity methods such as graph theoretical approaches since it adopts a unique data-driven and multi-step approach for constructing directed functional connectivity maps. The approach involves iterative *model building* and *pruning*. Initially, information from all participants is leveraged to establish a shared, group-level functional network map that reflects the majority of the sample. Group-level paths are retained only if they demonstrate significance for at least 75% of all individuals. This thresholding approach outperforms the common practice of averaging across individuals since it prevents the influence of individuals who significantly deviate from the sample. Simulation studies (Gates and Molenaar, 2012) have demonstrated that this threshold effectively detects true relations in the generated data more frequently than many competing methods, with minimal occurrence of false positives. All autoregressive paths are automatically estimated to accurately assess the directionality in the ROI paths (Lane & Gates, 2017). Once a shared, group-level functional network map is obtained, unnecessary paths are pruned at the group level. Additional paths at the individual level are then evaluated based on their ability to improve model fit for that specific individual. If individual-level paths do not significantly enhance the fit of the individual final model, they are pruned as well. The process of adding and removing paths is carried out using Lagrange multiplier test equivalents, or *modification indices* (Sörbom, 1989). Non-significant paths are removed at the individual level and discarded if they are not found in the group structure (Gates and Molenaar, 2012). Consequently, GIMME offers a distinct advantage by deriving a group-level map that is generally applicable to the majority of the sample, while allowing individual-level paths to emerge.

GIMME also has the ability to search for connectivity paths specific to subgroups. Subgroup-level analysis can be performed through two approaches: confirmatory subgroup GIMME (CS-GIMME) and subgrouping GIMME (S-GIMME) (i.e., exploratory S-GIMME). CS-GIMME identifies paths that

significantly improve the fit beyond the group model for predetermined subgroups using the same procedures as the group-level model building discussed above (Henry et al., 2019). In contrast, S-GIMME determines subgroup assignments in an unsupervised manner by analyzing individuals' connectivity maps (Gates et al., 2017). S-GIMME generates a similarity matrix based on group-level and candidate connections and applies the Walktrap community detection approach to identify clusters of individuals with similar paths (Gates et al., 2016, 2017; Pons & Latapy, 2005). Walktrap maximizes modularity within the sample and is robust to common issues in community detection. Walktrap provides a reliable method for subgrouping without relying on significance testing, which is challenging in network contexts.

Study 3 employed both CS-GIMME and S-GIMME to search for connectivity maps underlying emotion experience.

CS-GIMME: Supervised Subgrouping

CS-GIMME estimates connectivity maps for predetermined (a priori) groups. Predetermined subgroup assignments of time-series data may be based on existing theory or prior knowledge, representing specific hypotheses about the nature of the observed data (see Henry et al., 2019 for the validation of CS-GIMME). CS-GIMME accounts for any predetermined subgroup assignment during the model search procedure and identifies if similar patterns of connectivity exist within these subgroups. Here in Study 3, predetermined subgroup assignments hypothesize differences in functional connectivity between the factor conditions of emotion, situation, and culture; collectively, these conditions represent the within- and between-subject factors of the design matrix from which the observed data originate. We used CS-GIMME to determine whether meaningful patterns of connectivity are associated with each of the 8 subgroups, or the factorial of emotion (fear, sadness), situation (social, nonsocial), and culture (Chinese Asian, White American).

CS-GIMME begins with a group-level search to identify a connectivity map among ROIs that replicates for the majority of the sample. Once this shared, group-level connectivity map is obtained, CS-GIMME begins a subgroup-level search to identify a connectivity map among ROIs that replicate for the majority of individuals within a predefined subgroup. Thus, after identifying the group-level connectivity map that replicates for the majority of the sample, CS-GIMME proceeds to search for a connectivity map that replicates for the majority of individuals within a predefined subgroup (here, the 8 predetermined

subgroups of interest). In its final search stage, the individual-level search, CS-GIMME identifies additional path among ROIs that may be unique to certain individuals. As is done in the group-level search, the search for subgroup- and individual-level paths uses modification indices to identify significant ROI-to-ROI connections.

During the subgroup-level search, GIMME uses the group-level connectivity map as the null model with which to identify additional ROI-to-ROI paths that, if estimated for everyone in a subgroup, would improve the model fits for the greatest number of individuals in that subgroup. The addition of a path must significantly improve the model fits for the majority of individuals, and this is determined using Bonferroni-corrected p-values obtained from modification index tests. (The threshold for what constitutes the “majority” for the subgroup is defined by the researcher; here in Study 3, the threshold was the default used by GIMME, which is 75% of individuals for each subgroup). If a path is identified, it is estimated for everyone in the subgroup, with each path parameter (e.g., beta coefficient) estimated uniquely for each individual. The search for paths stops when no further paths can improve the model that represents the majority of individuals in the subgroup.

In its final search stage, the individual-level search, GIMME uses the group- and subgroup-level connectivity maps as the null models with which to identify any additional paths necessary to explain each individual’s functional connectivity map derived from time-series data. This process also employs modification indices, and paths with significant modification indices are added in a feed-forward iterative manner. The search for paths stops when no further paths can improve the model that represents the individual.

S-GIMME: Unsupervised Subgrouping

Subgrouping GIMME (S-GIMME) (Lane et al., 2021) builds on the GIMME unified SEM (uSEM) framework by using the Walktrap community detection algorithm (Pons and Latapy, 2005) to identify N subgroups of individuals who show shared connectivity patterns (see Fisher et al., 2023 for the validation of S-GIMME). S-GIMME also identifies paths that are unique to individuals. Subgroups are defined by a) having similar connectivity paths within block-Toeplitz (lag-1 and lag-0) correlation matrices as determined via the GIMME uSEM algorithm, and b) having paths with the same sign. We operationalized a subgroup as consisting of at least four individuals to ensure interpretability and reliability of the identified

subgroups (as in Doyle et al. 2022). We set this minimum criterion of 4 individuals per subgroup since smaller subgroups may reflect noise or idiosyncrasies that are not generalizable to the larger population.

Time-series data used in CS-GIMME were used in S-GIMME, but, unlike the CS-GIMME analyses, we provided no a priori information about the time-series data in the S-GIMME analyses. Without a priori information regarding factor conditions or individual characteristics, the objective with the unsupervised subgroup analysis was to identify meaningful clusters of individuals based solely on the time-series data. If subgroups were to emerge, subgroup membership would be treated as a dependent variable and (multinomial) logistic regression would be used to predict the probabilities of the different possible outcomes of subgroup membership. More specifically, if S-GIMME were to reveal subgroups derived solely from the time-series data, the resulting subgroup memberships would be regressed on the factor conditions of interest, as well as individual-difference measures.

Predictions

ROI-to-ROI Functional Connectivity Paths

We made no strong predictions for specific ROI-to-ROI functional connectivity patterns associated with particular emotions or contexts, since such estimations are inherently exploratory. However, given the apparent role of the default mode system in emotion (e.g., Doyle et al. 2022; Saarimaki et al. 2022), we expected differential connectivity in its nodes (DMPFC, MPFC/dACC, TP, and TPJ) across various emotions and situations (e.g., see Satpute & Lindquist, 2021). Moreover, considering the amygdala's role in integrating external sensory data and driving autonomic responses across emotional events (Barrett and Bliss-Moreau, 2009; Bickart et al., 2012; Cunningham and Brosch, 2012; Kim et al., 2011; Touroutoglou et al., 2014; Whalen, 2007), we expected that the amygdala may exert a direct effect on other ROIs, especially during visually-induced emotion experience (Lindquist et al. 2012). Indeed, fMRI evidence assessing functional connectivity during emotion shows that the amygdala impacts activity in other ROIs (Diano et al., 2017). Ultimately, we expected our exploratory investigation into directed functional connectivity to elucidate how certain ROIs may directly influence each other across diverse emotional contexts.

Supervised Subgrouping

Because Study 2 revealed some evidence that functional activation varied by a combination of emotion, situation, and culture, we predicted that functional connectivity patterns associated with emotion might also differ by these conditions. If there were different functional connectivity patterns associated with the interactions of emotion, situation, and culture, this would suggest that the factors manipulated in Study 2 are indeed key factors that moderate the neural network patterns associated with emotional experience. On the other hand, if the 8 conditions showed no significant difference in functional connectivity patterns, this would suggest that these factors do not substantially moderate the neural basis of emotion. Should CS-GIMME reveal identical functional connectivity patterns across multiple conditions of interest, we planned to assess whether the identified path structures differ significantly by condition, given that CS-GIMME's model search for one condition operates independently of other model searches.

Unsupervised Subgrouping

We predicted functional connectivity patterns that would differ by culture, but we made no a priori hypotheses about what other factors may structure the time-series data. For example, S-GIMME's group-level search may show that lateral regions in the prefrontal cortex (DLPFC, VLPFC) have a direct effect on other ROIs during emotion experience, whereas S-GIMME's subgroup-level search may show that cultural groups differ on the basis of DLPFC or VLPFC connectivity. This latter finding would be consistent with the abundant behavioral evidence showing significant differences in explicit and implicit self-regulation during affective experience between Chinese Asian participants and White American participants (e.g., Deng et al., 2019), insofar as DLPFC and VLPFC are both linked to executive functioning, including cognitive control (e.g., Brandl et al., 2019). In fact, in our prior dynamic causal modeling work using EEG, we found evidence for differential involvement of DLPFC during fear relative to neutral trials for Chinese Asian participants relative to White American participants. Specifically, the DLPFC's integration with other ROIs during fear experience was greater in Chinese Asian participants than in White American participants (Pugh et al. 2022).

Our primary interest in the unsupervised approach lies in whether cultural interactions or variations in emotion or situation impact directed functional connectivity, as this may corroborate any findings that emerge in the confirmatory analyses. In Pugh et al. (2022), we also found that self-identified

sex and culture were important factors in dynamic (directed) functional connectivity during fearful experiences. To test whether any factors or their interactions predicted subgroup membership, we regressed subgroup membership onto categorical variables of emotion (fear v. sadness), situation (social v. non-social), culture (Chinese Asian v. White American), sex (male v. female) and their interactions. Specifically, we employed multilevel logistic regression to predict subgroup membership based on said categorical variables, with the evocative conditions being nested within participants.

However, it is also possible that identified subgroups represent individual differences in other psychological factors such as attitudes related to cultural tightness as we observed in Study 2. This unto itself would be an important finding as there is emerging evidence that functional connectivity patterns associated with emotions are idiosyncratic (Koide-Majima et al., 2020) and presumably based on an individual's accumulated experiences over time. To address the role of individual differences, we conducted an exploratory multilevel logistic regression analysis to investigate the influence of individual differences in attitudes towards cultural tightness in the United States on subgroup membership. Our analysis included both the individual-difference measure and the evocative conditions as predictors, with conditions being nested within participants. Also included in the model were self-identified sex and cultural identity (Chinese Asian, White American). For detailed information on the individual-difference measure of cultural tightness, please refer to Table 4.2.

Lastly, previous research has shown that individual differences in affective state intensity may influence subgroup membership (Doyle et al. 2022). We thus performed a linear mixed-effects model to examine the effects of emotion, situation, subgroup membership, and their interaction on real-time emotional experience. We opted for a mixed-effects model for this particular analysis given the nested structure of the affective ratings (i.e., in-scanner ratings were nested within participants). Hence, a mixed-effects model allowed us to fit random effects to account for the nested structure of the data. Random intercepts were introduced for participants and stimuli. An overall analysis of variance (ANOVA) was then performed on the fixed effects model to assess the significance of the fixed effects in the model (see Bates et al., 2015 for an explication of using ANOVA with mixed-effects modeling).

Table 4.2: Cultural Tightness

Measure	Cronbach's α	Description	Example Items
Tightness-Looseness (TL; Mu et al., 2015)	0.88	Captures an individual's attitudes about social norms and rules within their society or group. Higher scores indicate views of a more rigid and rule-bound social environment.	"The United States is currently... too permissive, too restrictive." "Social Norms in the United States are currently... too flexible, too rigid."

Note. The TL scale ranged from 1 to 10, with two attitudes serving as anchors. For instance, in one of the examples provided, 1 represented "too permissive" and 10, "too restrictive."

Results

Group-level Search

A consistent group-level connectivity map was identified in both supervised and unsupervised procedures of GIMME. As shown in Figure 4.2 (black paths), group-level connectivity during negative emotional experience included significant paths linking bilateral amygdala, bilateral fusiform, bilateral medial OFC, and from right dalNS to right VLPFC. These paths reflect directed functional connectivity among these regions, indicating their shared functional role in instances of fear and sadness. All paths were significant for at least 75% of individuals. Notably, no regions evidenced paths with the amygdala.

For the subgroup-level search results, please see Figure 4.3 for a visualization of participants' contributions to different subgroups (confirmatory v. exploratory) within the conditions of interest. Below we further explain these results.

Supervised Subgrouping

We conducted a supervised search for meaningful sub-group level network connectivity patterns within eight a priori subgroups. A summary of the supervised subgrouping results can be found in Table 4.3, along with a list of the a priori subgroups under study.

No meaningful subgroup level connectivity map was identified for two a priori subgroups: "Nonsocial Fear" and "Social Fear" for White American participants. These findings suggest that beyond the group-level paths identified, there is significant variation in the neural representations of these conditions among White American participants.

Conversely, a common subgroup-level connectivity map was identified for five of the a priori subgroups: "Nonsocial Fear," "Social Fear," and "Nonsocial Sadness" for Chinese Asian participants, and "Nonsocial Sadness" and "Social Sadness" for White American participants. This subgroup-level connectivity map was characterized by a significant path from MPFC/dACC to DMPFC (wide, green path in Figure 4.2). We next sought to validate the distinctiveness of the common subgroup-level connectivity map among the five subgroups, given that the model searches for a priori subgroups operate independently and thus do not compare outcomes to solutions from other searches. To do so, we tested whether the individual estimates (i.e., beta coefficients) informing the identified path differed across the five subgroups. We found no evidence indicating the identified path differed significantly in magnitude

across the five subgroups ($F_{(4,108)} = 1.07$, $p = .374$), confirming that these subgroups provide no unique information regarding this path (i.e., MPFC/dACC → DMPFC). Rather, it seems this path underpins various affective states across individuals from two different cultures.

A subgroup-level connectivity map was also identified for one a priori subgroup: "Social Sadness" for Chinese Asian participants. This subgroup-level connectivity map was characterized by a significant path in the opposite direction of that identified above, from DMPFC to MPFC/dACC (narrow, green path in Figure 4.2). The connectivity map was significant for at least 75% of individuals in the subgroup, suggesting a distinct neural state associated with the experience of social sadness among Chinese Asian participants.

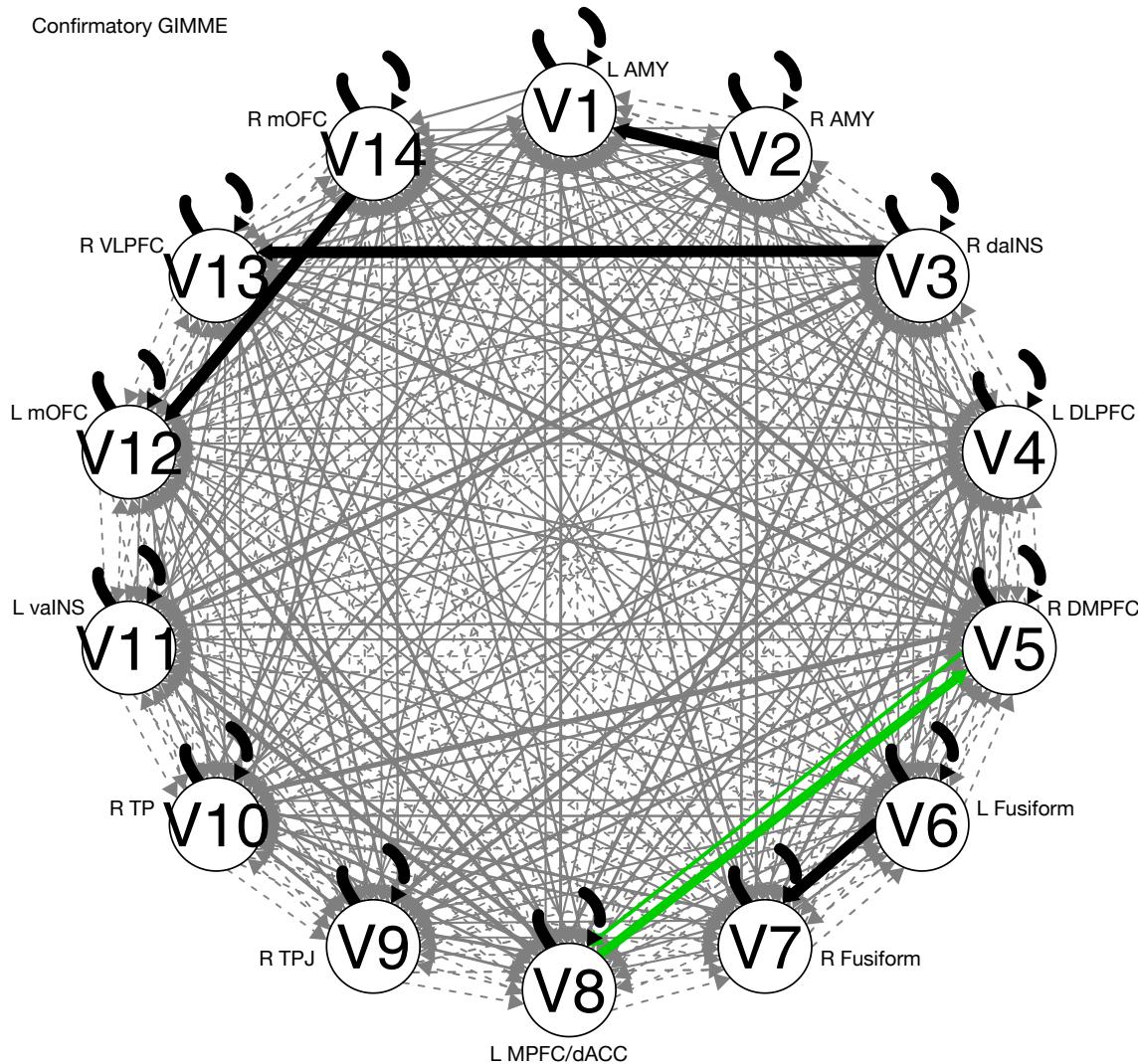
Table 4.3: Summary of Supervised Subgrouping Results

A Priori Subgroups	Identified	Identified Structure
1. Nonsocial Fear, Chinese Asian Ps	Y ^a	DMPFC ~ MPFC/dACC
2. Nonsocial Sadness, Chinese Asian Ps	Y ^a	DMPFC ~ MPFC/dACC
3. Social Fear, Chinese Asian Ps	Y ^a	DMPFC ~ MPFC/dACC
4. Social Sadness, Chinese Asian Ps	Y	MPFC/dACC ~ DMPFC
5. Nonsocial Fear, White American Ps	N	
6. Nonsocial Sadness, White American Ps	Y ^a	DMPFC ~ MPFC/dACC
7. Social Fear, White American Ps	N	
8. Social Sadness, White American Ps	Y ^a	DMPFC ~ MPFC/dACC

Note. Ps = participants. Y = yes; N = no. DMPFC = right dorsomedial prefrontal cortex. MPFC/dACC = left medial prefrontal cortex extending into the left anterior cingulate cortex. ~ = regressed on.

^a Although identified independently, these 5 subgroups show no significant difference in the identified structure.

Figure 4.2: Summary Plot for Supervised Subgrouping Analysis



Note. See Table 4.1 for ROI abbreviations. V = variable of interest. Gray represents individual-level paths, green represents subgroup-level paths, and black represents group-level paths. Width of paths corresponds to estimated path weight. The wider green path represents the common subgroup-level connectivity map identified for five of the eight a priori subgroups, whereas the narrower green path represents the subgroup-level connectivity map identified for one a priori subgroup (i.e., Social Sadness for Chinese Asian participants).

Unsupervised Subgrouping

We next conducted an unsupervised search for significant network connectivity patterns that operated solely on time-series data without any preexisting information about the data structure. A summary of the unsupervised results can be seen in Figure 4.4. The unsupervised search yielded two subgroups from the data; beyond the group-level path, an additional subgroup path existed only for Subgroup 2. Specifically, there was a significant path from MPFC/dACC to DMPFC (green path in Figure 4.4). The connectivity map was significant for at least 75% of individuals in the subgroup, suggesting a distinct neural pathway associated with negative emotional experience among Subgroup 2 participants. Descriptively, Subgroup 1 ($N = 34$) was composed of more White American ($n = 19$; 56% of the subgroup) participants than Chinese Asian ($n = 15$; 44% of the subgroup) participants. The association between sex, race, and subgroup membership for Subgroup 1 was examined using a chi-square test; this analysis revealed no significant difference in sex ($\chi^2 = 0.12$, df = 1, $p = 0.731$) or race ($\chi^2 = 0.471$, df = 1, $p = 0.493$) for Subgroup 1. On the other hand, Subgroup 2 ($N = 28$) was equally composed of both White American ($n = 14$; 50% of the subgroup) and Chinese Asian ($n = 14$; 50% of the subgroup) participants. The association between sex and subgroup membership for Subgroup 2 was also examined using a chi-square test; this analysis revealed no significant difference in sex ($\chi^2 = 0.14$, df = 1, $p = 0.706$). Notably, the conditions were not significantly driven by individuals' identities as some participants contributed data (conditions) to both subgroups; hence these participants ($N = 17$; 6 Chinese Asian, 11 White American) were found in both subgroups. These 17 individuals contributed some conditions (e.g., nonsocial fear) to either Subgroup 1 or Subgroup 2, whereas all other participants contributed all their conditions to either Subgroup 1 or Subgroup 2.

Because individuals were clustered into Subgroup 1 and Subgroup 2 based purely on time-series data, we next determined which factors best explained the generated subgroup assignments. For this purpose, we employed a series of multilevel logistic regressions to predict subgroup membership. We first regressed the generated subgroup assignments on the primary factors of interest: emotion, situation, culture, and self-identified biological sex. We included biological sex as a factor of interest since our previous work suggests it may potentially influence group membership in brain functional connectivity (see Pugh et al., 2022). We subsequently conducted an exploratory multilevel logistic regression with an

additional predictor, namely, the individual-difference measure on attitudes about cultural tightness. After we regressed subgroup membership on the primary factors of interest and the individual-difference measure to discern their influence on group membership, we regressed in-scanner affective responses on subgroup membership to discern how membership itself was related to real-time emotional experience.

First, a multilevel logistic regression model was fitted to predict subgroup membership based on condition (i.e., the emotion by situation conditions), culture, and sex; conditions were nested within participants. None of the predictors were statistically significant at the conventional alpha level of 0.05; neither emotion ($b = 0.19$, $SE = 0.31$, $z = 0.613$, $p = 0.540$), situation ($b = -0.28$, $SE = 0.31$, $z = -0.918$, $p = 0.359$), cultural identity ($b = -1.06$, $SE = 1.19$, $z = -0.89$, $p = 0.373$), nor self-identified sex ($b = -1.12$, $SE = 1.20$, $z = -0.94$, $p = 0.348$) predicted subgroup membership in this analysis.

Second, a multilevel logistic regression analysis was conducted to examine whether condition, cultural tightness, self-identified sex, or cultural identity were significant predictors of subgroup membership. A significant coefficient estimate would indicate the direction and magnitude of the relationship between the predictor and the log-odds of belonging to Subgroup 2.

No evidence was found to suggest that the evocative conditions ($ps > 0.062$), sex ($p = .613$), or cultural identity ($p = .742$) were significant predictors of subgroup membership. However, scores on attitudes of cultural tightness had a significant negative effect on subgroup membership ($b = -1.61$, $p = 0.031$). An increase in cultural tightness (i.e., viewing social norms in the United States are restrictive) was associated with a decreased likelihood of belonging to Subgroup 2.

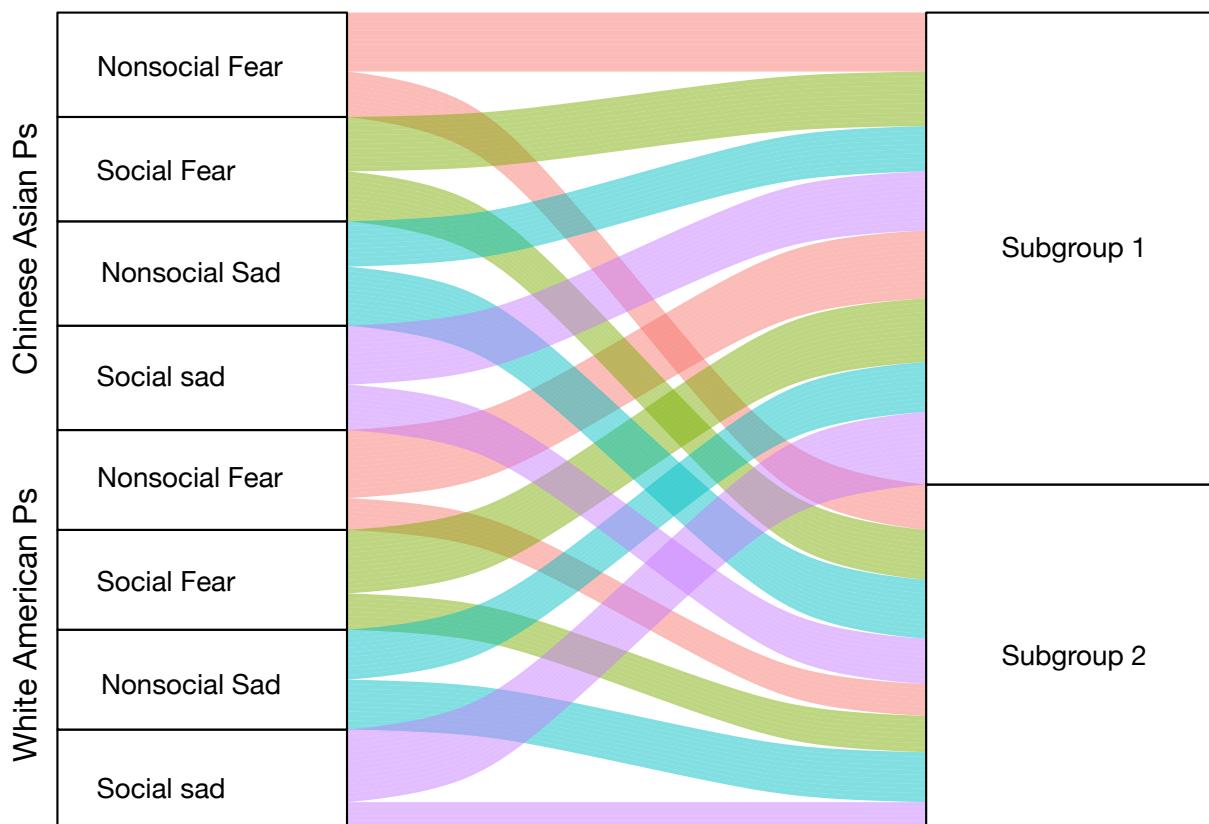
Third, a linear mixed-effects model was fitted to examine the effects of emotion, situation, subgroup membership, and their interaction on real-time emotional experience. The analysis included culture, sex, and stimuli ratings for valence and arousal as additional covariates. Random effects (intercepts) were also introduced for participants and stimuli. An overall analysis of variance (ANOVA) was performed to assess the significance of the fixed effects in the model.

ANOVA results showed a significant two-way interaction between emotion and subgroup membership ($F_{(3, 10751)} = 10.05$, $p < 0.001$). We probed this interaction via post-hoc pairwise comparisons. A pairwise comparison of subgroup membership within the fear condition revealed a significant difference

between Subgroup 1 and Subgroup 2 ($b = 0.13$, $SE = 0.024$, $z = 5.56$, $p < 0.001$). Subgroup 1 showed a higher response to fear stimuli compared to Subgroup 2. The subgroups also showed a significant difference within the neutral condition ($b = -0.12$, $SE = 0.024$, $z = -4.96$, $p < 0.001$). Subgroup 1 had a lower response compared to Subgroup 2; that is, Subgroup 2 reported relatively greater reactivity to neutral stimuli than Subgroup 1. The subgroups showed no significant difference within the sad condition ($b = -0.002$, $SE = 0.024$, $z = -0.089$, $p = 0.929$).

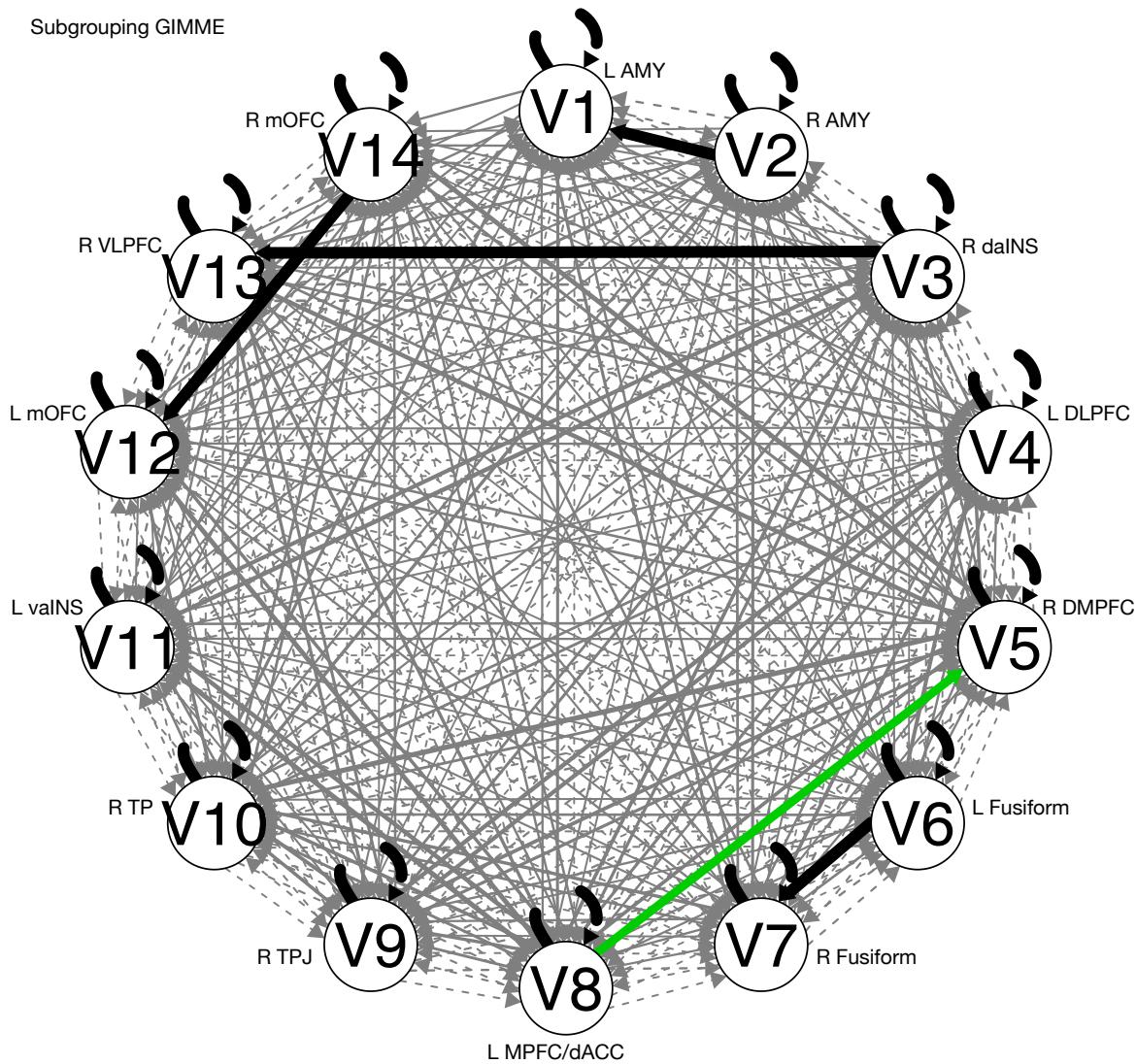
See Table 4.4 for a summary of the unsupervised subgroup findings.

Figure 4.3: Cross Over Between Confirmatory and Exploratory Subgroups



Note. The eight conditions on the left represent the eight predetermined groups submitted to CS-GIMME. In contrast, the two subgroups on the right represent the subgroups generated by S-GIMME. Each confirmatory condition (e.g., Nonsocial Fear) represents Chinese Asian ($n = 23$) or White American ($n = 22$) participants. Hence, Nonsocial Fear for Chinese Asian participants has 23 observations, some of which inform Subgroup 1 and others, Subgroup 2.

Figure 4.4: Summary Plot for Unsupervised Subgrouping Analysis



Note. See Table 4.1 for ROI abbreviations. V = variable of interest. Gray represents individual-level paths, green represents subgroup-level path, and black represents group-level paths. Width of paths corresponds to estimated path weight. The green path represents the connectivity map identified for Subgroup 2; no significant connectivity map was identified for Subgroup 1.

Table 4.4: Results of Multilevel Regression Models

Factors	Subgroup 1 v. Subgroup 2	Multilevel Model
Cultural Tightness	Perceiving greater cultural tightness in the United States was associated with a reduced likelihood of belonging to Subgroup 2. That is, perceiving stronger social norms and stricter expectations in the United States was associated with a decreased likelihood of belonging to Subgroup 2	Logistic
Fear Condition	Subgroup 1 showed greater emotional reactivity to fear stimuli than Subgroup 2. That is, Subgroup 2 was less reactive during instances of fear than Subgroup 1.	Linear
Neutral Condition	Subgroup 2 showed greater emotional reactivity to neutral stimuli than Subgroup 1. That is, Subgroup 2 was more reactive during neutral instances than Subgroup 1.	Linear

Note. This table summarizes differences that were observed between the two subgroups identified by the unsupervised procedure of GIMME (i.e., S-GIMME). For statistical output related to these findings, see pp. 110-111 of this document.

Discussion

The present study aimed to investigate the directed functional connectivity patterns associated with emotions and their situated representations using the Group Iterative Multiple Model Estimation (GIMME) method. We employed both confirmatory subgroup GIMME (CS-GIMME) and subgrouping GIMME (S-GIMME) to explore the factors underlying the brain representations of fear and sadness. Our findings provide valuable insights into the degeneracy of neural pathways associated with emotion, the impact of cultural and situational contexts on brain states, and the identification of meaningful subgroups based on functional connectivity patterns.

Degeneracy in Emotion

Constructionist theories of emotion posit that a single emotion category can be supported by multiple brain mechanisms, a phenomenon referred to as degeneracy (Barrett & Satpute, 2019; Edelman & Gally, 2001; Marder & Taylor, 2011; Sporns et al., 2000; Tononi et al., 1999; Whitacre & Bender, 2010). Previous investigations have indicated the existence of various neural pathways supporting the same

emotion category, such as anger and fear, in predominantly White North American participants (Doyle et al., 2022; Wager et al., 2015; Wilson-Mendenhall et al., 2013a). Our study bolsters this burgeoning body of evidence, demonstrating degeneracy in functional brain connectivity underlying social sadness in Chinese Asian participants.

The use of CS-GIMME allowed us to identify statistically differentiable patterns of connectivity between regions of interest that show consistent regional activation during emotion (e.g., Lindquist et al., 2012) and consistent cultural differences during social affective processing (Han & Ma, 2014). CS-GIMME identified a distinct subgroup-level connectivity pattern for Chinese Asian participants during social sadness. The neural representation of these experiences differed significantly for Chinese Asian participants, despite subjective social sadness experiences not showing significant differences between White American and Chinese Asian participants.

Constructionist theories of emotion hypothesize an effect of culture on the brain representations of emotions (see Lindquist et al., 2022), given that wiring of the human brain is heavily influenced by the immediate ecological environment, which varies across cultures (Atzil & Barrett, 2017; Atzil & Gendron, 2017; Chiao, 2018; Gendron et al., 2020). Our results suggest that cultural contexts contribute to meaningful variation in brain states associated with emotion. The uncovered path in our results indicated a direct effect from DMPFC to MPFC/dACC in Chinese Asian participants during social sadness. Although highly speculative, this neural path may suggest a behavioral tendency to use information from the immediate environment (e.g., conceptual abstraction, meaning-making) to interpret information in the self (e.g., visceral information from the body). This reasoning in fact aligns with extensive behavioral work showing a higher tendency among Chinese Asian participants to reference the context during self-referential processing than White Americans (De Vaus et al., 2018; Spencer-Rodgers et al., 2010; Yoo & Miyamoto, 2018).

Situated and Idiosyncratic Effects on Emotion

Human neuroscience studies show that situational contexts have a significant effect on the neural representations of emotion (e.g., Wilson-Mendenhall et al., 2011; Study 2 in this Dissertation). However, we found no influence of condition (emotion x situation) on brain connectivity in the unsupervised S-GIMME procedure at the conventional alpha level of 0.05. This null effect may suggest an insufficiency of

situational and emotional contexts alone to predict dynamic neural representations of emotions, which seem significantly variable. Perhaps this relates to behavioral studies in affective science, including meta-analytic work showing that emotion categories themselves are poor predictors of emotion experience and expression (Durán & Fernández-Dols, 2021). Perhaps emotion categories are poor predictors of dynamic emotional brain states (cf. Diano et al., 2017). On the other hand, we identified significant effects of emotion and situation in the supervised CS-GIMME procedure, with partial support provided by our CS-GIMME analyses. This outcome underscores, again, the role of cultural factors in shaping neural correlates of emotion. Although situational and emotional contexts alone may not have predicted functional connectivity associated with emotion experience, they did alongside cultural information.

Moreover, our findings indicated that individual-difference measures predict functional brain connectivity, revealing that subgroup membership is not solely determined by cultural or situational factors, but also reveals idiosyncratic variations among participants.

These findings underscore the complex, individualized nature of emotion-related brain connectivity. Specifically, we found that perceptions of cultural tightness were associated with dynamic functional connectivity associated with emotion. This unto itself is an important finding as there is emerging evidence that functional connectivity patterns associated with emotions are idiosyncratic (Koide-Majima et al., 2020) and presumably based on an individual's accumulated experiences over time. It is worth noting that Subgroup 2 consisted of equal amounts of Chinese Asian and White American participants, all of whom saw the US as having relatively loose cultural norms. These findings suggest that culture of origin per se may not predict emotional brain activity but that one's orientation to US cultural norms does.

Lastly, we found that individuals that showed a distinct neural connectivity pattern (MPFC/dACC to DMPFC) during negative affective experience were also less likely to be reactive to fear stimuli than individuals without said connectivity pattern. Although highly speculative, this suggests that individuals evincing the identified path may have been more likely to use their negative, subjective emotional experiences (MPFC/dACC) to retrieve contextualizing information (DMPFC) to assist with meaning-making (interpretation) of the evocative fearful stimuli. This reasoning extends itself to the finding that individuals with the identified path (Subgroup 2) were also more reactive to neutral stimuli than those without said path (Subgroup 1). Individuals in Subgroup 2 may have shown a stronger DMPFC to

MPFC/dACC connection because they may have accessed more emotional information about, or attributed more emotional meaning to, the evocative stimuli, including neutral stimuli.

Limitations

Although our study provides substantial insights, some limitations must be acknowledged. First, future research should extend the exploration to a wider range of emotions to provide a comprehensive understanding of neural pathway degeneracy. Second, our study primarily used self-reported intensity measures, and the inclusion of physiological and behavioral measures could offer a more holistic perspective on neural correlates of emotion. Third, our definition of culture was binary, and the dichotomy oversimplifies cultural complexity. Lastly, our situational context—social versus nonsocial—was also oversimplified. That said, the common denominator all social contexts is social information processing (Fan et al., 2021), and our operationalization accomplished that.

Conclusion

In conclusion, by utilizing GIMME, we found evidence for degeneracy in neural pathways, suggesting that diverse functional connectivity configurations can underpin identical emotional experiences. Further, cultural and individual factors were found to influence brain states associated with emotion, highlighting the influence of sociocultural factors on emotional processing. Our findings underscore the intricate and dynamic nature of emotion and pave the way for future research in sociocultural affective neuroscience.

CHAPTER 5: GENERAL DISCUSSION

This integrative dissertation encapsulates three distinct studies, all designed to probe the influence of contextual variables on the neural representation of emotions. By doing so, these studies challenge the implicit and explicit belief in affective neuroscience that the neural underpinnings of emotion are fixed and uniform. Instead, they illustrate the significant effect of context on the brain basis of emotion.

Cumulatively, these studies corroborate the constructionist perspective on emotions. They underscore the role of culturally-relevant concept knowledge in emotions (Barrett, 2006, 2022). Emotions emerge as complex, situated phenomena that depend not merely on internal processes but also on the surrounding context (e.g., Mesquita et al., 2010), including cultural information and the dynamic interplay between individuals and their environment (Lindquist et al., 2022). The studies illustrate the adaptable nature of emotion-related neural activity, emphasizing the necessity of acknowledging the influence of diverse contextual variables.

Study 1 investigated the impact of language and culture on the brain basis of emotion, considering language as a form of context that interacted with culture to represent and integrate culture-specific meanings of emotion concepts into on-going emotion perceptions. Study 1 found distinct differences in the neural substrates for emotion perception of disgust between Chinese Asian and White American participants, emphasizing the significant role of concepts in the construction of emotion perception and experience (Brooks et al., 2007; Doyle & Lindquist, 2021). By revealing that access to the word “disgust” altered functional connectivity between regions implicated in semantic retrieval, person perception, and social cognition in Chinese Native but not White American participants, Study 1 made the case that language influences emotion perception, with particular relevance for disgust in Chinese Asian participants. It elucidated that language, as a cultural artifact and a referent for concepts, substantially informs our understanding and perception of emotions (Lindquist et al., 2015; Pavlenko, 2017; Silverstein, 2004).

Study 2 shifted its lens to situational and cultural contexts, analyzing the influence of social versus nonsocial situations, cultural group membership, and cultural attitudes on the brain basis of emotional experiences. Study 2 demonstrated a significant influence of both cultural group membership and cultural attitudes on the brain basis of emotion. This investigation adds a new dimension to cultural neuroscience by endorsing the premise that culture operates on multiple fronts, encompassing discrete categories of group membership as well as individual attitudes towards societal norms, both of which emerge from enculturation and internalization of one's cultural milieu (Causadia, 2020; Erez & Gati, 2004; Klein & Kozlowski, 2000).

Study 3 employed directed functional connectivity maps and subgroup analysis to study experimental and individual-level factors influencing the neural representation of emotions. By distinguishing patterns of connectivity and identifying meaningful subgroups based on these profiles, the study brought to light significant individual variation in emotion-related brain connectivity beyond the factors studied in Study 2. The findings illustrated the intricate and highly personalized nature of emotions, underscoring the necessity of considering a broad spectrum of factors that extend beyond cultural or situational influences. However, it again revealed that cultural attitudes influenced the pathways underlying emotions, suggesting that for those individuals who move to the US from another country, their attitudes about the norms of their host culture may determine their resulting emotional processes to a greater extent than does the knowledge they acquired from their home culture.

Collectively, these studies underscored the significant influence of context on the neural representation of emotions. They challenged the existing notion of fixed neural signatures for emotions (e.g., Celeghin et al., 2017) and highlighted the role of socially-instantiated processes in emotion. In doing so, they replicate and extend many years of research in social psychology.

Social Psychology and Affective (Neuro)Science

Abundant behavioral research in social psychology demonstrates that the context in which people find themselves plays a significant role in shaping the social behaviors, perceptions, and experiences of those individuals. For example, given that social norms and expectations often shape how individuals behave in social situations (Chung & Rimal, 2016), the mere presence of other people can influence an individual's behavior (Karau & Williams, 1996; Torka et al., 2021), including their attitudes about risk-

taking, perceptions of danger and safety, and feelings of security over their decision-making (Chou & Nordgren, 2017). Extensive empirical research in social psychology furthermore shows that context effects are ubiquitous (e.g., see Mesquita et al., 2010, for a review). For example, a person's consumer behavior depends, in part, on their sunlight exposure—that is, on the time of day (Gullo et al., 2019); a person's everyday feelings seem to be closely linked not only to their personality, but also to their physical location (i.e., at home vs. at work vs. social gatherings) (Sandstrom et al., 2017); and Bond and Smith (1996), in their meta-analysis of 133 studies spanning 17 countries, found that people's level of conformity was a function of the temporal context (e.g., conformity steadily declined in the United States from 1952 to 1994) and cultural context (i.e., collectivist countries tended to show higher levels of conformity than individualist countries) (for a more recent example of temporal context effects, see Ofosu et al., 2019; for a temporal-by-cultural context effect, see Hamamura, 2012).

Moreover, research in social psychology has extensively recognized the impact of cultural contexts on shaping social behavior (e.g., Bond & Smith, 1996; Eid and Diener, 2001; Markus & Kitayama, 2010; Collardeau et al., 2022). Conceptual definitions of cultural contexts range on a continuum ranging from the most specific, tangible aspects of cultures (e.g., language, racial identities) to the most general, intangible elements of cultures (e.g., codified laws, implicit knowledge about social norms). This dynamic nature of cultural analysis, which can range from a micro level focus on the individual to a macro level examination of institutions and cultural milieus (Causadia, 2020; Erez & Gati, 2004; Klein & Kozlowski, 2000), is highlighted by Baldwin and Mussweiler's (2018) finding that US Americans' tendencies towards social comparison are largely influenced by state-level political conservatism and not solely by individual variation in the tendency for social comparison. In another study, with a sample of 13,573 of air traffic control staff from 21 national air traffic providers (i.e., 21 European countries), Tear et al. (2022) found that staff members with high social status (e.g., managers) were more likely to have positive perceptions of practices that maintain organizational safety (e.g., admitting error, challenging poor behavior) compared to members with low social status (e.g., administrative staff), and that these group-based differences in perceptions were intensified in countries that uphold established values for hierarchy and power.

A substantial amount of research in affective science has also established that cultural contexts play a significant role in shaping emotional events: The expression, perception, and experience of emotions are significantly dictated by the cultural and societal milieu in which individuals exist (De Leersnyder et al., 2020; Lindquist et al., 2022; Kitayama et al., 2020; Mesquita et al., 2017; Uchida et al., 2009). However, in contrast to the wealth of research in affective science, there has been a dearth of exploration in the field of affective neuroscience examining the influence of cultural contexts—and indeed, context in general—on the neural underpinnings of emotion. Given that contemporary emotional experiences are predominantly social (Boiger & Mesquita, 2014), and that the neural representations of social information processing exhibit considerable variability (Alcalá-López et al., 2018), it is logical to surmise that discrete emotional experiences within social contexts should demonstrate similar variability. This line of thought has served as a significant impetus for the present research. Our focus is to bridge the gap between affective science (heavily influenced by social psychology) and neuroscience, probing deeper into the role of cultural and social contexts in shaping the brain basis of emotion.

The Brain Basis of Encultured Emotion

A neural reference space for discrete emotion underpins an array of emotional perceptions and experiences (e.g., Lindquist et al., 2012). Notably, this neural reference space shows considerable overlap with the cultural neuroscience neural reference spaces showing cultural differences during social-cognitive tasks (self-referencing and mentalization) and social-affective tasks (emotion perception and emotion recognition) (Han & Ma, 2014; Shkurko, 2020). To date, no work has delved into the potential of these overlapping neural reference spaces for understanding the brain basis of emotion from a cultural affective neuroscience standpoint; the work in this dissertation did so by examining how culture and emotion together impact brain regions within these overlapping neural reference spaces. This novel approach, which merges cultural considerations with affective neuroscience, offers a unique opportunity to better comprehend how cultural context may shape the neural underpinnings of discrete emotional perceptions and experiences. The relatively unexplored intersection between these neural reference spaces holds immense potential for broadening our understanding of emotional processing within diverse cultural contexts.

Constructionist theory makes it possible to merge these seemingly disparate fields—cultural neuroscience and affective neuroscience. Constructionist theories of emotion assert that discrete emotion categories such as “fear” and “sadness” do not have consistent, unique behavioral action tendencies, facial behaviors, peripheral physiological signatures, or brain causal mechanisms (Baumeister et al., 2007; DeWall et al., 2016; Durán & Fernández-Dols, 2021; Jack et al., 2012, 2016; Siegel et al., 2018; Guillory & Bujarski, 2014; Lindquist et al., 2012; Wager et al., 2015). These theories suggest an inherent diversity in the associated actions, facial behaviors, physiological responses, and brain activity for any given emotion category such as “fear,” which are further influenced by the situation in which they occur and the cultural and societal norms that inform those experiences (De Leersnyder et al., 2020; Gendron et al., 2020; Hoemann et al., 2020; Lindquist et al., 2022).

Traditional emotion theories have often proposed that categories like fear encompass experiences sharing common causal mechanisms. Still, they overlook the culturally-driven variability in how emotions manifest or are perceived, or treat these processes as separate from the instantiation of the emotion itself. The concept of having centralized mechanisms producing specific emotions like fear has been extensively debated (Barrett & Satpute, 2013; LeDoux, 2014; Lindquist et al., 2012; Touroutoglou et al., 2015), yet the inclusion of cultural factors being a key area of discussion for the brain basis of emotion is rarely materialized (e.g., see Chiao, 2018; Qu et al., 2021). The central thesis of the integrative dissertation is that the heterogeneity in the neural basis of emotions is significantly influenced by cultural contexts, and context more generally (see Huang et al., 2018; Lindquist et al., 2012; Qi et al., 2018; Wager et al., 2015; Xu et al., 2021; Zheng et al., 2022). The Studies proposed provide support for that thesis.

Constructionist theories propose that emotions are “situated conceptualizations,” whereby the brain uses prior experiences, heavily influenced by cultural learning, to make sense of internal and external sensations as instances of specific emotions like “fear” or “anger” (Barrett, 2017; Wilson-Mendenhall et al., 2011). They emphasize that cultural context and language play a critical role in shaping our emotional experiences and perceptions—that is, in shaping situated conceptualizations (Lindquist & Barrett, 2012; Lindquist et al., 2015). Language, whether signed or spoken, is cultural (Blasi et al., 2022; Silverstein, 2004); signs and words serve as cues to emotional concepts. Culturally-informed language

helps guide predictions about inherently ambiguous affective states, aiding in the construction of emotional experiences and perceptions (Brooks et al., 2017). Hence, here, constructionist theories importantly spotlight the role of cultural context in both emotional experiences and emotion perceptions via language: A constructionist approach to emotions posits that emotional experiences and perceptions are interlinked as the brain uses semantic knowledge to refine culturally-infused sensory data into specific emotions relevant to the immediate context.

Regions involved in language usage and semantic retrieval are integral parts of the neural references identified in both affective and cultural neuroscience. These areas include the left inferior frontal gyrus (IFG; VLPFC) and anterior temporal pole (ATP), known for their roles in language production and comprehension, and semantic memory retrieval. By enabling us to label and discuss our emotions, these linguistic areas contribute significantly to the way emotions are formed, recognized, and understood, a process which is often culturally coded (Atzil & Gendron, 2017; De Leersnyder et al., 2017; Gendron et al., 2020; Lindquist et al., 2010; Mesquita et al., 2017; Uchida et al., 2020; Varnum & Grossmann, 2017).

Moreover, medial structures implicated in abstraction, meaning-making, and social cognition also contribute to these neural reference spaces. This includes regions such as the medial prefrontal cortex (MPFC), dorsal anterior cingulate cortex (dACC), and the posterior cingulate cortex (PCC), which are known to be involved in self-referential thinking, value-based decision making, and social understanding (Alcalá-López et al., 2018; Lieberman et al., 2019). These neural regions aid in the process of assigning meaning to emotions, relating them to self, and adapting them according to social norms and expectations. These same structures also play a significant role in cultural neuroscience (e.g., see Lin et al., 2018), given that cultural norms and values greatly influence the processes of abstraction, meaning-making, and social cognition (e.g., Baldwin & Mussweiler, 2018). For instance, a person's cultural background can affect how they interpret and respond to social cues, leading to differences in neural activation patterns within these medial structures (Lin et al., 2018).

Furthermore, the neural reference spaces these regions constitute are not static but are highly dynamic and context-dependent — in part, the present dissertation contributes to this understanding. These neural reference spaces change as we accumulate new experiences and learn from them (see

Atzil et al., 2018; Chiao, 2018; Qu et al., 2020). This adaptive nature of neural reference spaces underscores the significance of a culturally-contextual perspective in understanding the brain basis of emotion.

In conclusion, the overlap of neural reference spaces associated with language use, semantic retrieval, abstraction, meaning-making, and social cognition in affective and cultural neuroscience research may provide a richer understanding of how cultural contexts shape the neural basis of our emotional experiences; it may also provide a framework by which degeneracy in human brain function emerges.

Limitations and Future Directions

Although the conducted studies provide valuable insights into the influence of contextual variables on the neural representation of emotions, certain limitations should be acknowledged. First, the sample composition was Chinese Asian and White American participants, which may restrict the generalizability of the findings to other cultural groups. The choice to sample these cultural groups was made to leverage the extensively used “East-West” paradigm in cultural psychology and neuroscience, which has allowed for a fruitful understanding of cultural differences in various behavioral domains, including emotion (e.g., see Kitayama & Markus, 2010). Additionally, we aimed to advance this paradigm by grounding the discrete operationalization of culture (“Chinese vs. White”) in social psychological research and constructionist theory. Both social psychology and constructionism suggest that discrete categories acquire meaning through internalization and conceptualization over one’s lifetime, consequently influencing individuals’ perception of the world (Firat, 2021). It is noteworthy that this approach to discrete categories, such as “Chinese” or “White,” is rare in cultural neuroscience studies, as they are typically accepted at face value without deeper examination (see Denkhaus & Bös, 2012 and Martínez Mateo et al., 2012 for discussions). Moreover, we introduced a novel operationalization of culture alongside the “East-West” paradigm by examining attitudes of cultural tightness, highlighting the social psychological nature of this variable and its impact on people’s feelings and expressions, often beyond conscious awareness (e.g., Lopez et al., 2022). We show that this variable has an effect on the brain basis of emotion. Nonetheless, we acknowledge the limitations of the “East-West” paradigm and recognize the existence of other cultural factors that are not captured within this model. Therefore, future

research should explore alternative cultural paradigms. Additionally, expanding the participant pool to include individuals from diverse cultural backgrounds would allow for a more comprehensive investigation of how context influences the neural representation of emotions across a broader range of populations.

Second, the sampling of Chinese individuals living in China could yield different results compared to the Chinese Asian participants residing in a Western cultural context. The acculturation process and exposure to different cultural norms in the host country might impact individuals' emotional processes and neural representations; indeed, our findings on cultural tightness suggest this may be the case. Sampling Chinese individuals in their home country could offer valuable insights into the influence of cultural context, without the potential confounds associated with acculturation. It would be interesting, for example, to explore variations in attitudes of cultural tightness within a Chinese sample and examine how these attitudes relate to neural activity associated with emotion. It is possible that individuals perceiving a tight environment would recruit regions associated with attention or self-regulation (e.g., DLPFC) during emotion experience. If so, this would replicate our results and further suggest that the impact of culture on the neural basis of emotion is more related to one's perceptions and attitudes toward the surrounding environment (context) above and beyond their cultural identity (e.g., Chinese). Future studies could also aim to include participants from both China and Chinese individuals residing in different cultural contexts (excluding North America and China) to investigate potential variations in the neural representation of emotions based on cultural environments.

Relatedly, our sample of Chinese Asian participants living in the United States may underestimate the degree of cultural differences that exist in brain activity associated with emotion experience. Indeed, previous work suggests that individuals who voluntarily move to a different country or culture may *a priori* resemble members of the new, host culture on certain psychological dimensions (Feng et al., 2017). Yet our examination of individual differences in perceptions of social norms in the United States provides some insight into the cultural factors that influence neural responses to emotional events. Specifically, we were able to examine individual differences in perceptions of cultural tightness in the United States, which predicted Chinese Asian—but not White American—participants' neural responses in the DMPFC and DLPFC. Those Chinese Asian participants who perceived the United States to have quite tight cultural norms presented a neural profile that is consistent with what individuals

from prototypically “collectivist” cultures might be expected to show (e.g., see de Grecq et al., 2012); that is, Chinese Asian participants in the present study showed greater activation in brain regions associated with attention and behavior regulation and the representation of others’ mental states during emotion. It is interesting that this was the case in our task, even when there was no explicit goal to regulate one’s emotions (e.g., see Davis et al., 2012). We are unsure, however, why some individuals from mainland China perceived the United States to have tighter cultural norms. One hypothesis is that these individuals may have been less acculturated to their host nation than those Chinese Asian individuals who perceived the United States to have looser social norms. Alternatively, those who perceived tighter cultural norms might have selected to move to the United States for different reasons than those who perceived it to have looser social norms (e.g., exclusively to pursue educational opportunities v. because they wished to live in a nation with looser norms). Future research should explicitly examine the impact of emotional acculturation on brain activation (as in behavioral studies; e.g., De Leersnyder et al., 2011) and more generally unpack individual differences within culture that could drive brain activity.

Third, the ecological validity of the experimental paradigms employed in the studies needs to be addressed. Although efforts were made to simulate contextual influences (e.g., the presence of social information in the immediate context), the controlled MRI setting does not capture the complexity and dynamics of real-life emotional experiences and perceptions (cf. Holleman et al., 2020, 2021). Future research could explore more ecologically valid approaches, such as naturalistic settings using functional near-infrared spectroscopy (fNIRS), to provide an additional representation of how context influences the neural underpinnings of emotions. For example, studies could involve interactive social situations or emotionally relevant scenarios while participants’ neural activity is recorded using fNIRS. This approach would allow for the examination of emotions as they naturally unfold, taking into account the dynamic interplay between individuals and their environment. By studying emotions in such ecologically valid settings, we can gain deeper insights into how context influences the neural representation of emotions.

Fourth, this dissertation is limited in its scope of multilevel context factors. The neural basis of emotion is influenced by a multitude of factors operating at different levels, including individual, interpersonal, and societal factors (Han et al., 2015; Veissière et al., 2020; Wang, 2021). These multilevel factors can significantly shape the neural representation of emotions (see Lindquist et al.,

2022). At the individual level, factors such as personality traits, prior emotional experiences, and cognitive processes can impact how emotions are processed and represented in the brain. These individual differences may introduce variability in neural responses to emotional stimuli and influence the extent to which contextual variables modulate emotional processes. Indeed, results from Study 3 suggest individual differences play a significant role in the neural basis of emotion. By accounting for such individual-level factors, and by explicitly operationalizing them as context variables (see Barrett et al., 2011 and Greenaway et al., 2018 for discussions), future research can provide a more nuanced understanding of how individual-level context factors contribute to the neural representation of emotions. Furthermore, interpersonal factors, including social relationships, cultural norms, and social influence, also play a crucial role in shaping the neural basis of emotion. The studies presented here have started to explore the influence of cultural attitudes on emotional processing, but additional interpersonal factors, such as social support, social hierarchies, and cultural practices, should be considered to gain a more comprehensive understanding of the social dynamics that impact the neural representation of discrete emotion categories. Future research could investigate how these interpersonal factors interact with other contextual variables (e.g., individual level factors) to shape emotional neural responses.

Moreover, societal factors, including cultural values, social institutions, and socioeconomic contexts, can influence the neural basis of emotion. While the studies presented in this dissertation have touched upon the influence of cultural factors, it is important to acknowledge that cultural contexts are multifaceted and dynamic. Cultural values differ within cultural groups (e.g., see Na et al., 2010), and the impact of cultural context on emotion varies across different societal contexts (e.g., see Jackson et al., 2019). Future research could delve deeper into the interplay between cultural, institutional, and socioeconomic factors to explore how these multilevel influences shape the neural representation of emotions. To mitigate the limitations associated with said multilevel factors—individual, interpersonal, and societal—future research could employ longitudinal designs to capture changes in the neural representation of emotions over time and examine how multilevel factors dynamically shape emotional processing, including experience and perception. Additionally, incorporating a broader range of emotions beyond the negative emotions studied here, employing other neurophysiological measures and tools

(e.g., fNIRS), and sampling of various cultural groups at different developmental stages would enhance our understanding of the neural basis of emotions in diverse contexts.

Implications and Conclusion

Findings of the current work challenge the notion of invariant neural correlates of emotions. The implicit and explicit notion that emotions have invariant neural correlates assumes that specific emotions are consistently associated with distinct patterns of neural activation across individuals and contexts (for a discussion, see Lindquist et al., 2012). This belief in fixed and universal neural signatures of emotions has guided much of affective neuroscience research in the past, and continues to do so (e.g., see Celeghin et al., 2017; Gu et al., 2019; Panksepp et al., 2017; see also Ortony, 2022 for a discussion). By demonstrating the impact of language, culture, and situational factors on the neural basis of emotions, the studies presented here refute the notion of invariant neural correlates and highlight the dynamic and context-dependent nature of emotional processes. The findings underscore the need to consider a broad range of contextual variables when examining the neural underpinnings of emotions.

At minimum, the research presented in this dissertation has implications for current work in psychiatric models of emotion. Traditional psychiatric models often assume a universal and fixed neural basis for emotions, which informs our understanding and treatment of affective disorders (e.g., see Maté, 2022; Power and Dalgleish, 2015). However, the present dissertation highlights the significant influence of contextual variables on the neural representation of emotions, suggesting that prevailing models of emotion may oversimplify the complexity of emotional processes in psychiatric conditions (see Aldao, 2013). Indeed, a reaction to this oversimplification has been the rise of cultural psychiatry, a branch of psychiatry that emphasizes the role of cultural context in shaping mental disorders (e.g., Kirmayer, 2007). Because this dissertation emphasizes the significance of incorporating cultural factors into the study of the neural underpinnings of emotions, such an approach holds relevance for cultural psychiatry, as it too recognizes the necessity of considering cultural factors in comprehending and diagnosing emotional disorders. By recognizing that the neural bases of emotions can vary across cultural contexts, psychiatric models will need to incorporate cultural influences to provide a more accurate and inclusive understanding of emotional disorders in diverse populations.

Furthermore, the adaptable (degenerate) nature of emotion-related neural activity revealed here and elsewhere (e.g., Doyle et al., 2022), raises questions about the stability and reliability of neural markers used in psychiatric assessments and diagnoses. If the neural correlates of emotions are highly context-dependent, it becomes necessary to consider the specific contexts and conditions under which individuals with emotional disorders are assessed. This challenges the assumption that specific neural patterns can be universally associated with specific psychiatric conditions and underscores the importance of considering the influence of contextual factors in psychiatric assessments, including individual, interpersonal, and societal factors.

Overall, the present dissertation challenges the assumptions underlying traditional psychiatric models of emotion, highlighting the dynamic and context-dependent nature of the neural basis of emotions. Integrating these insights into psychiatric models, particularly through the lens of cultural psychiatry, can enhance our understanding and treatment of emotional disorders by accounting for the influence of contextual factors. Ultimately, this dissertation advocates for a paradigm shift towards a context-aware approach in affective neuroscience (see Barrett, 2022; Willems & Peelen, 2021), one that acknowledges the dynamic interplay between emotions, neural processes, and the broader ecological and sociocultural context.

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