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5	Culture and Gender Modulate dlPFC Integration in the Emotional Brain: Evidence from Dynamic Causal		
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Abstract

25 Past research has recognized culture and gender variation in the experience of emotion, yet this has not 26 been examined on a level of effective connectivity. To determine culture and gender differences in 27 effective connectivity during emotional experiences, we applied dynamic causal modeling (DCM) to 28 electroencephalography (EEG) measures of brain activity obtained from Chinese and American 29 participants while they watched emotion-evoking images. Relative to US participants, Chinese 30 participants favored a model bearing a more integrated dorsolateral prefrontal cortex (dlPFC) during fear 31 v. neutral experiences. Meanwhile, relative to males, females favored a model bearing a less integrated 32 dlPFC during fear v. neutral experiences. A culture-gender interaction for winning models was also 33 observed; only US participants showed an effect of gender, with US females favoring a model bearing a 34 less integrated dIPFC compared to the other groups. These findings suggest that emotion and its neural 35 correlates depend in part on the cultural background and gender of an individual. To our knowledge, this 36 is also the first study to apply both DCM and EEG measures in examining culture-gender interaction and 37 emotion. 38 39 Keywords. Emotion, fear, culture, gender 40 41 1. Introduction 42 **1.1 Emotion is situated** 43 Emotion categories are not monolithic entities but are highly situated phenomena (Barrett, 2017; 44 Ellsworth, 2013; Mesquita et al., 2016). There is evidence that feelings (Coifman et al., 2016), behaviors 45 (Y.-P. Chang & Algoe, 2020), physiology (Kreibig, 2010; Siegel et al., 2018) and cognitions (Power & 46 Dalgleish, 2015) accompanying emotions can vary substantially across contexts. There is also evidence 47 that emotional brain states vary across stimulus type (Yuan et al., 2019), situation (Wilson-Mendenhall et 48 al., 2011), personality traits (Lim et al., 2012), cultural background (Kwon et al., 2013), and gender

49 (Fischer et al., 2004).

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In the present study, we contribute to the extant research on individual differences in emotion by

51 examining how culture, gender, and their interaction alter the effective connectivity in emotional brain 52 states. Culture describes the socioecological context that individuals are exposed to throughout their 53 lifetime, as well as the values, norms, icons, and beliefs to which people adhere (Eagly, 2013; Gelfand et 54 al., 2017; Markus & Kitayama, 1991). Gender refers to the meanings that individuals within a culture 55 ascribe to male and female categories (Wood & Eagly, 2002). There is evidence that emotion emerges 56 from the interaction of broadscale networks spanning prefrontal, paralimbic, limbic, and sensory cortices 57 that support basic processes such as the generation of visceral states, representation of semantic 58 knowledge and cognitive control (Barrett & Satpute, 2013; Cunningham et al., 2013; Lindquist & 59 Barrett, 2012b; Pessoa, 2018; Satpute & Lindquist, 2019). The specific combination of these networks is 60 highly situated and is influenced by factors such as culture and gender (Barrett, 2017; Wilson-61 Mendenhall et al., 2013). Yet relatively little research has examined how culture, gender, and their 62 interaction influence effective connectivity between brain regions during emotional experience.

63 To this end we apply a dynamic causal modeling (DCM) analysis to electroencephalography 64 (EEG) recordings obtained from participants viewing fear-eliciting and neutral images. In contrast to 65 imaging techniques such as fMRI, EEG offers a unique advantage of high temporal resolution needed to 66 capture the causal dynamics of emotion processing (Gevins, 1997; Nam, 2020). Unlike functional 67 connectivity, which measures correlations of activity among brain regions, DCM is a measure of 68 effective connectivity, allowing us to quantify the directed influences among neuronal populations in a 69 brain network and make inferences of causal influence between those brain regions (Brown & Friston, 70 2012; Friston et al., 2003; Huang & Nam, 2020; Kiebel et al., 2008). The emotion category of fear was 71 chosen as an example of an unpleasant, high arousal emotion; the neural correlates of unpleasant 72 affective experiences (Lindquist et al., 2016) and fearful experiences (Lindquist & Barrett, 2012) have 73 been extensively studied. Because of the strong association between the amygdala (responsible for 74 attending to and resolving uncertainty in the environment, including threats; Adolphs, 2008) and fear 75 experience (itself an instance of threat and uncertainty), the amygdala and its connections provided a 76 straightforward starting point for developing a model space for fear, comprising a set of frontal-limbic 77 regions including the dorsolateral prefrontal cortex (dlPFC), anterior cingulate cortex (ACC),

ventromedial prefrontal cortex (vmPFC), and primary visual cortex (V1).

79 By focusing on how remote neuronal dynamics influence or cause each other in different 80 contexts-rather than limiting our interpretations to mean-level regional activity that is more commonly 81 reported in analyses of brain activity (Kim et al., 2017, 2019; Wittenberg et al., 2017)—DCM can extend 82 our understanding of the neural processes (functional integration of the brain) that underlie human 83 emotional experience. We hypothesized that the effective connectivity networks would differ between 84 male and female participants and between US and Chinese participants. To our knowledge, no 85 neuroimaging study has simultaneously examined the roles of both culture and gender with respect to the 86 causal functional architecture of emotional experiences.

87 **1.2 Effects of Culture, Gender, and their Interaction on Emotion**

88 Cultural background has been repeatedly implicated in emotion generation and regulation. For instance, 89 how emotion is externalized and communicated-to include language, facial expression, vocalization, 90 and posture-is known to vary across cultures (Gendron, 2017). Bonassi et al. (2021) found that 91 Japanese participants' categorization of emotion in facial expression varies with the expressor's ethnicity. 92 A language of one culture may encode different meanings for emotion categories in a manner that does 93 not align with other cultures (Jackson et al., 2019). Culture-bound syndromes have been documented, 94 such as ataque de nervios (Guarnaccia et al., 1989), hwabyeong (Chiao et al., 2013), and taijin kyofusho 95 (Kleinknecht et al., 1997; but see also Suzuki et al., 2003). Such emotion words play a role in 96 conceptualization of emotion during the construction of emotional experiences, which then shape 97 emotional processing at the level of neural networks (Brooks et al., 2016).

In addition to emotion conceptualization, studies in social psychology and neurophysiology have found that emotion regulation varies with culture, a finding often attributed to the cultural variation along an individualist-collectivist dimension: whereas Eastern cultures prioritize harmony with the group, Western backgrounds value independence and individuality (Butler et al., 2007; de Greck et al., 2012; Han & Ma, 2014; Lindquist & Barrett, 2008; Park & Huang, 2010). In one study involving an emotion suppression task, Asian participants showed significantly lower late positive potential compared to European American participants, corroborating an account of culturally ingrained emotion regulation 105 (Murata et al., 2013). Much of this research has implicated the dorsolateral prefrontal cortex (dlPFC) 106 (Han & Ma, 2014), a region involved in the central executive network and implicated in emotion 107 regulation (MacDonald et al., 2000). Still, to our knowledge the effect of culture on effective 108 connectivity of emotional brain states has yet to be investigated. Given the cultural differences in the 109 recruitment of the dlPFC in emotion regulation and given the cultural differences in the emphasis on 110 emotion regulation, our first hypothesis (H1) is that compared to US participants, Chinese participants 111 will show greater involvement of prefrontal regions during instances of fearful experiences.

112 Gender is another thoroughly studied dimension of individual differences in emotion. A 113 common finding has been that females tend to self-report stronger negative affect than males (Fujita et 114 al., 1991; Knyazev et al., 2010; Ma-Kellams & Wu, 2020; Zhang et al., 2017). Greater self-reported 115 negative affect in women is also associated with more sustained amygdala responses to multiple 116 presentations of negative stimuli (Andreano et al., 2014), and women consistently show greater amygdala 117 activity to negative stimuli than men across the neuroimaging literature (Stevens & Hamann, 2012). 118 These differences may be related to differences in amygdala-prefrontal connectivity: in a task involving 119 negative stimuli, women self-reported more extreme negative affect while men showed higher amygdala-120 dmPFC connectivity than women; the degree of amygdala-dmPFC connectivity was inversely correlated 121 with enculturated gender roles such as participants' degree of self-endorsed femininity (Lungu et al., 122 2015). In a study measuring resting state amygdala connectivity, women showed relatively greater 123 connectivity between amygdala and structures such as the putamen and precuneus, and men showed 124 relatively greater connectivity between amygdala and superior temporal gyrus and inferior frontal gyrus 125 (Engman et al., 2016). Another study found greater amygdala-IFG connectivity in women compared to 126 men (Kogler et al., 2016). In an explicit emotion regulation task involving reappraisal strategy, women 127 and men showed similar levels of self-reported affect following regulation, but women showed less 128 attenuation of amygdala and greater IFG and dlPFC activation (McRae et al., 2008).

Although findings of sex differences in structural and functional connectivity have been found elsewhere (e.g., the pars triangularis; see Keresztes et al., 2021 and Rubin et al., 2017), differences of prefrontal-amygdala connectivity appear especially relevant to our investigation of emotion. Therefore, our second hypothesis (H2) is that effective connectivity between amygdala and medial prefrontal regions (ACC, vmPFC) will differ between males and females. To our knowledge, only one study has examined gender differences in effective connectivity of emotion experience, namely using Granger causality analysis (Lungu et al., 2015). In this regard, our DCM analysis of gender makes a novel contribution to the literature.

Considering gender differences in emotion and the centrality of culture in socialization, it is worth questioning the persistence of these differences across cultures. Reviewing studies of cross-cultural gender differences in personality, cognitive, and physical traits, Schmitt (2015) showed that most evidence favors explanations implicating an interplay of evolution and sociocultural influences, as opposed to strictly socialization as an explanation. Moreover, he observed a counterintuitive trend wherein more egalitarian cultures show greater sex differences.

143 Studies involving self-report have found culture to interact with gender in their influence on 144 emotion. For instance, Zhao et al. (2019) observed a culture-sex interaction wherein Australian females 145 were uniquely high in self-report empathy, showing greater scores than Mainland Chinese females and 146 Australian males, while no significant difference was found between Australian and Mainland Chinese 147 males. In a follow-up study, Zhao et al. (2021) found the same culture-sex interactions in trait empathy, 148 as well as several interactions in state empathy wherein Australian females showed stronger empathy 149 response than Australian males on several emotion categories. Concerning fear, they found that Chinese 150 female participants scored higher on state empathy than female Australian participants when shown 151 instances of male and female fear, and they scored higher than Chinese male participants for instances of 152 female fear, although they also caution that they had obtained a low empathic accuracy for fear in that 153 study.

Bagozzi et al. (1999) found that women's self-reported experience of negative and positive affect was found more likely to embody the norms of their cultures; women from collectivist cultures were more likely to experience positive and negative affect as independent, whereas women from individualist cultures were more likely to experience them as bipolar opposites. Another study spanning 37 countries found a robust gender-specific pattern in which women reported more powerless emotions (i.e., fear) than men, but they also found interaction between gender and the country's rated gender equality, such that women from cultures with greater gender equality reported more dominant emotions (i.e., anger) (Fischer et al., 2004). In a task involving explicit emotion regulation in response to negative emotional images, Chinese men and American women reported the lowest and highest levels of emotion, respectively (Davis et al., 2012). Chinese men reported using disengagement strategies to regulate their emotions more than any other group. However, another study found no effect of culture or gender after controlling for depressive symptoms (Kwon et al., 2013).

However, neuropsychological investigations of culture-gender interaction and emotion are sparse. Given the past self-report evidence demonstrating culture-sex interaction (Zhao et al., 2019, 2021), and ample evidence of culture and gender individually influencing emotion, our third hypothesis (H3) is that gender and culture will likewise be interactive in their influence on the effective connectivity in the brain during fear vs neutral experience.

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2.1. Participants

2. Method

174 Twenty-three United States natives of European-American descent (mean \pm SD: 21.2 \pm 1.5 years, 12 175 females) and 13 Chinese natives who had lived in Mainland China for at least 18 years (mean \pm SD: 21.9 176 \pm 2.1 years, seven females) participated in the study. Time lived in Mainland China was included to rule 177 out the possibility of significant enculturation. Gender was evaluated as a dichotomous variable and there 178 were no participants who self-identified a gender different from their biological sex. All participants were 179 native or proficient English-speaking participants who reported having no history of neurological 180 disorder and normal or corrected-to-normal vision. Among Chinese participants, there were no 181 significant gender differences in time lived in China or in the US. All participants were right-handed. 182 Handedness was controlled as it is known to influence brain lateralization (Toga & Thompson, 2003), 183 and hand preference was assessed using the Edinburgh inventory (Oldfield, 1971). Participants provided 184 written informed consent and were given monetary compensation for their participation. The study 185 protocol was approved by the University's Institutional Review Board.

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187 2.2 Procedure

188 This study examined the same EEG dataset as an earlier study implementing Granger causality analysis 189 on the influence of culture and situation on emotion (Pugh et al., 2021). The image set comprised 180 190 colored images selected from the International Affective Picture System (Lang et al., 1999). This 191 included 60 images for each of the emotion categories fear, sad, and neutral. For this study, only neutral 192 and fear images were examined to obtain a fear-neutral contrast. Sad images were excluded for the 193 purpose of having a manageable model space. Emotion categorizations were based on normative ratings 194 obtained from participants on Amazon's Mechanical Turk (N = 444; 54% female, $M_{age} = 37.13$ years, SD = 11.48). For fear images, the average rating for fear was greater than the average rating for the other 195 emotions. Normative ratings of valence for fear differed significantly from neutral images (F = 169.51, p 196 < 0.001). The arousal level of fear differed significantly from neutral arousal levels (F = 494.42, p < 197 198 0.001).



Figure 1 Schematic of stimulus sequence and timing of the task. At the beginning of each trial, cross fixation was displayed for 4 seconds, followed by an affective picture for 4 seconds, and then emotion rating scale were presented for 4 seconds. The total duration of each trial was 12 seconds regardless of

203 conditions.

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Images were arranged in five runs, with each run comprising 36 images. Images were presented on a 17" computer screen placed 60 cm in front of the participants. Each image was presented for 4s following a 4s fixation period (Fig. 1). Participants were asked to report their levels of emotion (from 1 to 5) after each image presentation.

209 Participants were first presented with a practice trial for task familiarization. Afterwards, an 210 EEG cap was fitted to the participant and the main trials began. After the experiment, participants 211 completed a nine-minute resting state task during which they were asked to focus on the fixation on 212 screen and keep their mind at rest.

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214 **2.3. EEG Acquisition and Pre-processing**

215 EEG signals were recorded using a 256-electrode EEG cap (Electro-Cap International, Inc.) with 62 216 active electrodes arranged according to the modified 10-20 system (Sharbrough et al., 1991). Recordings 217 were referenced to the left ear lobe and grounded between AFz and Fpz. EEG signals were amplified 218 with g.USBamp amplifiers (g.tec Medical Engineering), sampled at 256 Hz. The EEG data was 219 preprocessed and analyzed using MATLAB (The MathWorks, 2004), EEGLAB (Delorme et al., 2011), 220 and SPM (Litvak et al., 2011). EEG signals were bandpass filtered between 0.01 and 75 Hz to examine 221 only relevant frequency bands. Artifact subspace reconstruction (ASR) was applied to identify and 222 remove artifacts (C. Y. Chang et al., 2018). We performed channel interpolation to reject bad channels as 223 well. The data was then re-referenced to an average reference for further analysis.

Following data collection and pre-processing, DCM was implemented in four steps: ROI selection, model specification, parameter estimation, and model comparison. The general procedure of DCM is outlined in Appendix A.

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228 **2.4 Selection of regions of interest**

229 Five regions of interest (ROIs) were selected based on their functional connectivity at rest (Bickart et al.,

230 2014; Roy et al., 2009) and during instances of fear (Baczkowski et al., 2017; Zhang et al., 2017). As the 231 first ROI, the amygdala bears structural and functional connectivity with regions of the prefrontal cortex 232 (including dIPFC and ACC) (Phillips et al., 2008) and visual cortex (Amaral et al., 2003). It thus serves 233 as a hub to multiple brain networks essential to supporting perception and behavior during affective 234 states (Bickart et al., 2014). Although subcortical areas are not typically the targets of evoked response 235 EEG measures, sources embedded in the limbic area (e.g. amygdala) can be included in a DCM analysis 236 for MEG/EEG model along with other cortical sources, as the interactions between the deep sources and 237 sources close to the scalp can be inferred from DCM (Attal et al., 2012; J. Li et al., 2021).

238 The prefrontal cortex is thought to implicitly regulate amygdala function (Delgado et al., 2008; 239 Diekhof et al., 2011; Gee et al., 2013; Hänsel & von Känel, 2008; Motzkin et al., 2015; Phan et al., 240 2002), and prefrontal-posterior coupling as measured by EEG is known to be taxed in conditions where 241 different emotion-evoking images are presented (Hao et al., 2019). As a second ROI, the vmPFC was 242 selected for its structural and functional connectivity with the amygdala (Bickart et al., 2014; Phillips et 243 al., 2008; Porrino et al., 1981). As a third ROI, the dIPFC was selected for its role in the central executive 244 network, as well as its role in regulating emotion in tandem with the anterior cingulate cortex (ACC) 245 (MacDonald et al., 2000; Phillips et al., 2008). The dlPFC does not bear strong direct anatomical 246 connections with the amygdala (Delgado et al., 2008; Ray & Zald, 2012), but it has been implicated in 247 tasks of explicit emotion regulation (Banks et al., 2007; de Greck et al., 2012; Morawetz et al., 2016; 248 Ochsner et al., 2002) and may be involved in recruitment of semantic knowledge during the emotion 249 generation and regulation (Lindquist et al., 2012). As a fourth ROI, the ACC bears connections with the 250 amygdala (Bickart et al., 2014), and the dorsal ACC is involved in tasks demanding attention modulation 251 (Hariri et al., 2003). As a fifth ROI, the visual cortex was selected for the nature of our stimuli and its 252 well-known structural connectivity with the amygdala (Amaral et al., 2003). Visual processing is 253 modulated by emotional stimuli (Aguado et al., 2012; Padmala & Pessoa, 2008; Vuilleumier & Driver, 254 2007), and the amygdala has been found to enhance visual encoding of form and motions associated with fearful expressions (Furl et al., 2013). 255

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ROI coordinates were chosen based on previous studies on fearful emotion modulation for

- amygdala (Furl et al., 2013), regulatory effect of vmPFC (Motzkin et al., 2015), ACC (Shi et al., 2019),
- and dIPFC (Kim et al., 2019). The mean locations for the nodes are listed in Figure 2. Coordinates were
- based on the MNI space coordinates for the corresponding region (Lacadie et al., 2008).
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No.	Region	MNI Coordinate	
1	l-Amygdala	-24, 0, -21	
2	r-Amygdala	21, -1, -22	
3	I-ACC	-5, 39, 20	5 4 6
4	r-ACC	6, 33, 16	
5	I-vmPFC	-11, 38, -19	7 8
6	r-vmPFC	12, 37, -19	10 A 10 A 10
7	I-dIPFC	-39, 34, 37	
8	r-dIPFC	35, 39, 31	
9	I-V1	-11, -81, 7	9 10
10	r-V1	11, -78, 9	

Figure 2 Prior locations for the regions considered for DCM models. Sources of activity were modelled as equivalent dipoles (estimated posterior moments and locations). Their prior mean locations are superimposed in an MRI of a standard brain in Montreal Neurological Institute (MNI) space in mm

266 **2.5 Model specification**

A model space was created comprising eight models varying in extrinsic connections between the selected ROIs. Models varied primarily in the manner of connectivity among the dIPFC, vmPFC, and ACC (Figure 3).



Fig. 3. The model space. Double arrow means reciprocal connections. amygdala (AMY); dorsolateral
prefrontal cortex (dlPFC); ventromedial prefrontal cortex (vmPFC); anterior cingulate cortex (ACC);
primary visual cortex (V1).

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274 Two models (#1a and #1b) excluded the dlPFC entirely, two models (#2a and #2b) incorporated 275 the dIPFC in serial connection between V1 and the other two frontal regions, two models (#3a and #3b) 276 incorporated the dIPFC as working independently from the ACC and vmPFC, and two models examine 277 two extremes of dIPFC involvement: exclusive involvement of dIPFC (#4) and a dIPFC that is fully 278 integrated with the other frontal regions (#5). The first and second-group models entertain the possibility 279 that the dIPFC affects the amygdala either not at all or indirectly, consistent with findings of neuroanatomical connectivity (Ray & Zald, 2012). Furthermore, within the first, second, and third 280 281 groupings the models varied in the presence of a vmPFC-ACC connection. In this way, integration of the 282 dlPFC was tested fairly independently of vmPFC-ACC connectivity.

As an additional model specification, we adopted Jansen's neural-mass model (Jansen & Rit, 1995), which describes each brain source in terms of the average post-membrane potentials and mean firing rates of three neuronal subpopulations corresponding to one of three cortical layers and their mutual inhibitory and excitatory connections.

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288 **2.6 Parameter estimation**

289 Bayesian model selection (BMS) was used to determine winning models for each group of culture and 290 gender-Chinese, US, females, and males-as well as their factorial combinations. Log-evidence value 291 was used to quantify the model plausibility (Garrido et al., 2007; Penny et al., 2004). The log-evidence 292 indicates which of the pre-established models, or connectivity patterns, best explains the dataset in a 293 manner that is both accurate (due to the accuracy term) and parsimonious (due to the complexity term). 294 For group comparisons log-evidence values are simply summed to obtain a group value. Between two 295 log-evidence values, a difference of at least three is regarded as strong evidence in favor of the winning 296 model (Garrido et al., 2007; Kiebel et al., 2008; Penny et al., 2004). Finally, the average connectivity

297 parameters across models were calculated for estimating the coupling among brain regions using 298 Bayesian model averaging (BMA). BMA is weighted by the posterior probability for each model, 299 meaning that models with greater probability contribute more to the average than models with lower 300 probability.

We also examined coupling gains and conditional probabilities for each connection. A coupling gain indicates a directed connection's gain in connectivity in response to exogenous input perturbation (i.e., experimental stimuli). Higher gains indicate greater gain in connectivity strength, or greater effective connectivity. Positive and negative gains indicate excitatory and inhibitory causal influence, respectively (Friston et al., 2003). A gain is often reported alongside a probability value, indicating the conditional probability of a gain surpassing a threshold value (Garrido et al., 2007).

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3. Results

309 3.1. Winning models

Bayesian model selection (BMS) was used to determine winning models for each group of culture and gender. As shown in Figure 4, there were culture-based differences in the winning models. For Chinese participants, the winning model was the one with the fully integrated dIPFC (Model #5), while for US participants the winning model was one in which the dIPFC was relatively less integrated with other cortical structures (Model 3b). The crucial difference between these models is the presence of dIPFC-ACC and dIPFC-vmPFC connections, which are present in #5 and absent in #3b.

Differences in evidence between the winning model and the second model were significant for both Chinese participants ($\Delta F = 706$) and US participants ($\Delta F = 127$), although US participants showed an apparently close competition among models #3a, #3b, and #5. Compared to the other two models, #3a is unique in the absence of a vmPFC-ACC connection. That is, all three of these models showed direct dlPFC-amygdala connection, with their only differences being the presence of connections among the frontal regions dlPFC, vmPFC, and ACC.





Figure 4. Results of Bayesian Model Selection (BMS) for (a) culture and (b) gender groups. The graphs show an approximation (the free-energy) of log-evidence (i.e. the log of the model evidence). Values are relative to the model with lowest log-evidence (model #4). Asterisks indicate the winning models in each group; Δ F indicates differences in log-evidence between the best model and the second optimal model.



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Figure 5 Results of Bayesian Model Selection (BMS) for each combination of culture and gender on emotional processing. US-Male (N = 11), US-Female (N = 12), Chinese-Male (N = 6), Chinese-Female

(N = 7). Asterisks indicate winning models within each group. The graphs show an approximation (the free-energy) of log-evidence (i.e. the log of the model evidence). Values are relative to the model with lowest log-evidence (model #4). Asterisks indicate the winning models in each group; ΔF indicates differences in log-evidence between the best model and the second optimal model.

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335 The winning model for females was the direct-connection model #3b, while that for males was 336 the fully-integrated model #5 (Figure 5). These are the same two winning models as with the culture 337 comparison, with the difference being the presence of dlPFC-vmPFC and dlPFC-ACC connections. Both 338 winning models significantly outperformed their second-place competitors ($\Delta F = 512$ for females, $\Delta F =$ 339 489 for males). For females, a close second model was #3a which again is the same as model #3b with 340 the exception of a missing vmPFC-ACC connection. To examine the interaction of culture and gender, 341 we conducted similar BMS procedures for male and female data of Chinese and US participants (Figure 342 6). For Chinese participants, the winning model is the fully integrated model (#5) regardless of gender $(\Delta F = 190 \text{ for females}, \Delta F = 516 \text{ for males})$; the parallel model (#3b) is a relatively close second place 343 344 for Chinese females. For US participants, a gender difference was observed with males having the fully 345 integrated model (#5) as winning and females having a parallel model (#3b) as winning. For US females 346 as well, the winning model was marginally higher than model #3a.

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348 **3.2 Parameter estimates**

349 Using BMA, coupling gains were obtained for the winning model of each group of culture and groups of 350 gender (see Figure 6 for visual summary; see supplementary materials for precise gain values and 351 posterior probabilities). For instance, a gain of .082 from l-amygdala to ACC would indicate an 8.2% 352 increase in effective connectivity fear images, as opposed to neutral images, are presented. To 353 concentrate on non-trivial connections, we focus our attention on gains exceeding 0.1 in value and 354 bearing a posterior probability greater than 0.95 (Bönstrup et al., 2016). This criteria allowed us to reduce 355 our scope of discussion from 64 connections to 15 for the culture comparison, and from 64 connections 356 to 11 for the gender comparison.



Figure 6 Significant coupling gains estimated for each connection in the best (or winning) model as a function of culture (a) and gender (b). Left and right networks correspond to left hemisphere and right hemisphere, respectively. Color represents coupling gain, or change in effective connectivity in fear vs neutral conditions (> 95% posterior probability). Green = significant positive gain; red = significant negative gain; black = nonsignificant gain. For thicker arrows, coupling gain \ge .1; otherwise coupling gain < .1.

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Because of differences in winning models for culture and gender, comparisons of their coupling gains cannot be made. Likewise, culture-gender interaction shows a unique winning model for US females, and this precludes a comparison of this group's parameters with other groups. However, comparisons of groups bearing model 5 is still feasible; this includes Chinese females, Chinese males, and US males.

Figure 7 shows coupling gains and posterior probabilities for the factorial combinations of culture and gender. For groups bearing model 5, Chinese females showed the largest number of strong connections (18), followed by Chinese males (13) and US and males (7). Coupling gains from the amygdala were especially strong for the Chinese female group; of the six connections, four were strong and significant (to 1-ACC = 0.126, r-ACC = -0.133, 1-vmPFC = -0.196, 1-dlPFC = -0.147). For connections to the amygdala, Chinese males exhibited strong connectivity to the right amygdala from all three frontal regions, though only two were significant (from ACC = -0.171, vmPFC = -0.205). Correspondingly, Chinese females showed strong connection to the amygdala from r-ACC-amygdala (-0.154) and 1-dlPFC-amygdala (-0.145). US males showed strong connections to the left amygdala from 1-ACC (-0.175) and 1-vmPFC (-0.126).

For connections from the dIPFC, Chinese females showed strong connections to 1-amygdala (-0.145), 1-ACC (0.154), and 1-V1 (0.149). Chinese males showed strong connection from r-dIPFC to ramygdala (0.106) and r-V1 (0.205), though the former connection fell short of significant. US males did not show strong connections to or from the dIPFC. Chinese females showed strong significant connections to 1-dIPFC (from 1-amygdala = -0.147, 1-V1 = -0.348, r-V1 = -0.349) and to r-dIPFC (from r-ACC = -0.136, r-vmPFC = 0.103).

For connections with V1, Chinese females showed the greatest number of strong from-V1 connections (5). Strong connections to V1 were most frequent in both Chinese males (3) and females (3). US males showed no strong to-V1 connection.



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Figure 7 Significant coupling gains estimated for each connection in the best (or winning) model of each culture-gender pairing. Left and right networks correspond to left hemisphere and right hemisphere, respectively. Color represents coupling gain, or change in effective connectivity in fear vs neutral conditions (> 95% posterior probability). Green = significant positive gain; red = significant negative gain; black = nonsignificant gain. For thicker arrows, gain \geq .1; otherwise gain < .1.

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4. Discussion

397 The purpose of this study was to examine the role of cultural background and gender on emotion 398 experience in terms of effective connectivity among a set of brain regions consistently linked to 399 emotions. To this end, we applied DCM to EEG data, leveraging advantages of high temporal resolution 400 that could not be offered by other imaging methods. Consistent with previous studies, our results 401 confirmed that fear is associated with effective connectivity amongst prefrontal, amygdala, and occipital 402 regions. Consistent with a constructionist account, we also demonstrated for the first time that this 403 effective connectivity is modulated by participants' culture of origin and gender, as well as an interaction 404 between the two. We discuss these findings in further detail, beginning with the interaction effect of 405 culture and gender, pertaining to H3.

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407 4.1 Interaction of culture and gender on connectivity during fearful experiences

408 Our main expectation (H3) was that culture and gender would interact to influence effective connectivity, 409 and this was confirmed with a finding that US female group exclusively showed a winning model that 410 did not bear dIPFC-vmPFC or dIPFC-ACC connections. That is, US females were differentially affected 411 as a function of their gender and cultural background, with US males, Chinese females, and Chinese 412 males bearing a common winning model wherein the these connections were present.

413 Though the count of significant connections is too granular for a quantitative statistical analysis, 414 it is worth noting that Chinese females showed the greatest number of strong connections, followed by 415 Chinese males. One notable difference concerned coupling gains from the amygdala, which was more 416 consistently negative for Chinese females compared to Chinese males and US males. As an additional 417 follow-up analysis for groups bearing model 5 as the winning model, we compared the amy-dlPFC and 418 dlPFC-amy coupling gains between Chinese females and Chinese males, and between Chinese males and 419 US males (Figure 8). Our post-hoc test revealed a significant difference between these Chinese females 420 and Chinese males in the amy-dlPFC connectivity strength (t(16) = -5.65, p < .001). This was unexpected 421 considering the effect of gender, wherein females overall showed a winning model without a dIPFC-422 amygdala connection. A second difference was a consistent negative couplings in connections to the 423 dlPFC from bilateral amygdala, bilateral V1, and r-ACC in Chinese females, while in Chinese males 424 these gains were more heterogeneous.

Altogether, US females were markedly different from the other four groups in the relative absence of two connections in their winning model. Chinese females demonstrated the strongest response to fear images, and they alone showed strong inhibitory connection from the dlPFC to the amygdala in either hemisphere. This is reminiscent of a finding in an earlier study that women of eastern and western cultures occupied extremes in terms of self-reported affective experiences, with females aligning most strongly with their culture, while males were less extremely different (Bagozzi et al., 1999). Insofar as dlPFC connectivity could reflect automatic regulation, Chinese females align most strongly with a 432 cultural drive to regulate emotion, while US females do not. Additionally, gender differences in the l-433 amygdala-dlPFC were found across culture, with gains that are positive gains for males and negative 434 gains for females. Given that the reverse connection was not significantly different across cultural 435 groups, it is possible that this difference reflects differences between males and females in the 436 amygdala's role in directing attention.

437

438 **4.2 Effect of culture on connectivity during fearful experiences**

Regarding culture, our hypothesis (H1) was that Chinese participants would demonstrate greater involvement of prefrontal regions compared to US participants. This was confirmed by the finding of cultural differences in winning models (Fig. 4). Chinese participants had the fully integrated dlPFC model (#5) as their winning model bearing dlPFC-vmPFC and dlPFC-ACC connections, while US participants had a parallel connection model (#3b) in which dlPFC was not connected to ACC and vmPFC as their winning model.

Thus, for Chinese participants, the dIPFC appears to be more strongly affected in its connectivity with other regions during the experience of fear. An interesting point is that for all groups, the winning model bore a direct connection in effective connectivity between the dIPFC and the amygdala, despite a known lack of anatomical connection between the two regions (Ray & Zald, 2012). One possibility is that dIPFC exerts effects on amygdala via other regions we did not examine. Either way, for US participants alone the dIPFC appears to have had effective connectivity with amygdala in the absence of simultaneous vmPFC and ACC connectivity.

A common explanation for cultural differences in emotion regulation has been that the collectivist aspect of Eastern cultures more strongly encourages group conformity, which entails regulating one's own emotions (Butler et al., 2007; de Greck et al., 2012; Lindquist & Barrett, 2008; Park & Huang, 2010). The constructionist account of emotion holds that emotion is an emergent product of interactions between networks responsible for creating visceromotor states in the service of adaptive responses (in this case, the amygdala) and networks responsible for interpreting stimuli and bodily input in terms of semantic knowledge (i.e., the conceptualization network) (Barrett, 2011). Differences of 459 culture include both semantic knowledge of emotion-laden concepts and selection of appropriate 460 responses. Such differences would likely manifest themselves as differences in brain regions supporting 461 the representation and use of conceptual knowledge as well as the selection of behavioral responses, such 462 as the vmPFC, ACC and dlPFC. Insofar as these regions also project to the visual cortex (Barrett & Bar, 463 2009), differences in conceptualization could influence predictions about the meaning of visual stimuli.

Altogether, BMS established connectivity differences between Chinese and US participants in terms of winning models, while differences in amygdala-dlPFC connectivity strengths could not be compared due to differences in winning models. Future research should examine in greater detail the specific mechanisms underlying differences of amygdala-dlPFC connectivity.

468

469 **4.3 Effect of gender on connectivity during fearful experiences**

470 We also expected (H2) that males, compared to females, would show differences in connectivity between 471 medial frontal regions (ACC, vmPFC) and amygdala, based on previous research showing greater 472 functional connectivity between dmPFC and amygdala in males. However, while males and females 473 differed in their winning models for connectivity, they both favored models bearing all three connections 474 to the amygdala. The key difference between the models involved dlPFC-vmPFC and dlPFC-ACC 475 connections, which were present in the male group's winning model and absent in the female group's 476 winning model. This suggests that for females the dIPFC had less of an influence to and from both ACC 477 and vmPFC. Future research might examine these unexpected differences.



Figure 8 Coupling gains obtained by Bayesian model averaging are graphed for (a) C2 connection from
Amy to dlPFC at LH by (b) comparison of C2 for groups bearing model 5 as the winning model. *p <
.005. LH, left hemisphere; dlPFC, dorsolateral prefrontal cortex; Amy, amygdala. Note that US_F group

is not included, as their winning model was different from the other three groups and thus preventedvalid comparison.

483

484 **4.4 Implications for affective computing**

485 Beyond implications for neuropsychology, there are a couple of implications for affective computing, the 486 design of human-computer interaction systems capable of inferring human emotion from facial 487 expression and other biological and behavioral measures (Poria et al., 2017). Analyses of EEG-measured 488 connectivity and activation patterns show promise in categorizing emotion (P. Li et al., 2019). As a 489 means of analyzes effective connections, the prospect of applying DCM to emotion classification 490 systems is a prospect worth exploring. A second implication is that, while much of the emotion 491 recognition efforts has leaned toward a one-size-fits-all approach to emotion recognition (Picard, 2003; 492 Poria et al., 2017), the evidence presented here converges with earlier evidence from neuropsychology 493 and social psychology in support of the account that emotion is constructed in a manner highly bound to 494 individual traits, namely, cultural background and gender. Classification accuracy has already been 495 shown to improve when accounting for gender (Rukavina et al., 2013; Vogt & André, 2006) and age 496 (Rukavina et al., 2016). The prospect of incorporating culture in classification systems is also worth 497 exploring.

498

499 4.5 Limitations

We acknowledge a limitation of sample size; however, previous DCM studies have demonstrated strong 500 501 effects examining comparably small sample sizes (Huang et al., 2021; Kim et al., 2017, 2019; Protopapa 502 et al., 2014; Sato et al., 2001), and our sample proved sufficient to establish significance among many 503 connections. Previous DCM studies have likewise shown uneven sample sizes (e.g., Cooray et al., 2016). 504 In terms of technical limitations, a 64-channel analysis is relatively coarse compared to analyses 505 employing more channels. However, previous DCM research has proved successful in using this number 506 of channels (Babajani-Feremi et al., 2012; Legon et al., 2016). As another limitation, DCM does not 507 allow the comparison of parameters across different winning models, and this prevented a more thorough

analysis of culture-gender interaction. Future studies should further examine the fronto-limbicconnections implicated in the winning model differences.

510 We also acknowledge limitations in our operationalization of culture and gender. There is the 511 question of cultural representativeness, given that the recruitment of Mainland Chinese participants living 512 in the US raises the question of possible enculturation. Our recruiting criteria aimed at discounting this 513 possibility, but a more controlled method would have been to recruit participants in their home countries. 514 We also categorized participants based on self-reported gender since gendered socialization is a form of 515 enculturation. While gender is non-binary and norms in the field are beginning to shift, our study still 516 reflects the present norms in the field (Abbruzzese et al., 2019; Keresztes et al., 2021). Lastly, a 517 limitation of scope was imposed by a need for tractability, and so not every emotion-relevant region of 518 the brain was examined, and moreover only one emotion category in our paradigm was examined. For 519 instance, future work might examine the pars triangularis, which was recently implicated studies 520 examining sexual dimorphism in structural connectivity (Keresztes et al., 2021) and sex differences in 521 the influence of hormones (Rubin et al., 2017). Nevertheless, our application of DCM was fruitful in 522 helping to clarify the hierarchical relationships between brain regions in negative emotion modulation 523 among people from different cultural backgrounds and of different gender. It provides a basis for future 524 development and improvement in understanding the social-biological loop of human information 525 processing.

526

527

5. Conclusion

To summarize, we investigated the influence of culture and gender on emotion—specifically fear—by measuring the effective connectivity among brain regions of a frontal-limbic-amygdala-visual network. We found that connections among prefrontal regions—and in particular with the dlPFC—vary across culture and gender, with Chinese females showing especially strong connectivity from the amygdala to frontal regions and US females favoring a model with relatively sparse integration of the dlPFC with other frontal regions. These results provide further support for an approach that accounts for the situated nature of emotion. To our knowledge, this is also the first investigation of culture-gender interaction through the lens of EEG and effective connectivity via the DCM method.

536

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