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Title

Altered effective connectivity from the posterior insula to the amygdala mediates the relationship between psychopathic traits and concern with the Harm foundation

Author names and affiliations

Shuer Ye^{1,2#}, Wei Li^{1,2#}, Bing Zhu³, Yating Lv^{4*}, Qun Yang^{1,2*}, Frank Krueger⁵

¹ Department of Psychology, School of Education, Hangzhou Normal University, Hangzhou, China

² Institute of Psychological Science, Hangzhou Normal University, Hangzhou, China

³ School of Marxism, Zhejiang Yuexiu University, China

⁴ Centre for Cognition and Brain disorder, the affiliated Hospital of Hangzhou Normal University

⁵ Department of Bioengineering, George Mason University, Fairfax, VA, USA

*Corresponding authors:

Yating Lv, lvuyating198247@gmail.com; Qun Yang, qunyang@hznu.edu.cn

[#] The two authors contributed equally to the research.

Manuscript Information

Number of pages:30| Number of figures/tables:5/3| Number of words for Abstract/

Manuscript:195/4790

Keywords

psychopathic traits, harm, effective connectivity, insula, amygdala

24 **Abstract**

25 Psychopathic traits have been demonstrated to be associated with different types of
 26 morality; however, the neuropsychological mechanism underlying the relationship
 27 between psychopathic traits and morality remains unclear. Our study examined the
 28 effective connectivity (EC) of psychopathic traits-related brain regions and its
 29 association to concern with different moral foundations by combining behavioral
 30 measures with resting-state fMRI. We administered the Levenson Self-Report
 31 Psychopathy Scale (LSRP) and Moral Foundation Questionnaire (MFQ) to 78 college
 32 students after resting-state fMRI scanning. Our results showed that total and primary
 33 psychopathic traits score predicted concern with the Harm foundation. The EC from
 34 the posterior insula to the amygdala was negatively correlated with psychopathic traits
 35 and positively with concern with the Harm foundation. Altered posterior insula-
 36 amygdala EC partially mediated the relationship between psychopathic traits and
 37 concern with the Harm foundation. Our findings indicated that individuals with
 38 elevated psychopathic traits may have atypical processes in recognizing and
 39 integrating bodily state information into emotional responses, leading to less concern
 40 for harm-related morality. The study deepened our understanding of the
 41 neuropsychological mechanism underlying the relationship between psychopathic
 42 traits and morality and may have implications for the prevention of higher
 43 psychopathic traits individuals from committing serious transgressions.

44

45 **Keywords:** psychopathic traits; moral foundations; Granger Causality; amygdala,
 46 posterior insula

47 INTRODUCTION

48 Psychopathy has been recognized as a personality disorder, primarily characterized by
 49 problematic interpersonal relations, shallow affect, poor behavioral control,
 50 irresponsibility, and disregard of moral norms (Hare, 1991, 2003). There are two
 51 subtypes of psychopathy, including primary psychopathy and secondary psychopathy.
 52 Primary psychopathy is associated with interpersonal and affective features whereas
 53 secondary psychopathy is linked to aggressive and antisocial lifestyles (Hare, 1991).
 54 Psychopathy has been increasingly recognized as a continuum of personality traits
 55 rather than a taxonomic feature (Corr, 2010). Those who are not clinically identified
 56 as psychopaths, but with higher psychopathic traits, may also show typical
 57 psychopathic characteristics (Brennan et al., 2018; Djeriouat & Trémolière, 2014;
 58 Neumann & Hare, 2008).

59 Individuals with elevated psychopathic traits may engage in various immoral
 60 behaviors, posing challenges to societies in maintaining social order (Beaver et al.,
 61 2017). Therefore, the relationship between psychopathic traits and moral cognition is
 62 of great interest to many researchers (Blair, 2007; Gao & Tang, 2013; Marsh et al.,
 63 2011). Moral Foundation Theory (MFT), a widely known framework on human
 64 morality, provides a new perspective for investigating the relationship between
 65 psychopathic traits and morality (Gay et al., 2018). According to this theory, morality
 66 consists of five foundations: (1) Harm (preventing harm to others); (2) Fairness
 67 (preserving fairness, equal rights, and justice); (3) Loyalty (practicing loyalty to one's
 68 own group); (4) Authority (respecting authority and social order); and (5) Purity
 69 (pursuing purity or sanctity of body, mind, and soul) (Haidt, 2012; Haidt & Graham,
 70 2007).

71 Psychopathic traits have been consistently shown to be associated with concern

with different moral foundations (Aharoni et al., 2011; Fernandes et al., 2020). This relation was especially pronounced for the Harm and Fairness foundations (Aharoni et al., 2011; Glenn et al., 2009a; Marshall et al., 2018). Individuals scoring higher in psychopathic traits are significantly less likely to endorse the Harm and Fairness foundations in the community (Glenn et al., 2009a) and forensic samples (Aharoni et al., 2011). Furthermore, emotion may serve as a mediator in the relationship between psychopathic traits and morality (Glenn et al., 2009a; Patil, 2015; Ye et al., 2021). For example, a lower level of empathic concern predicts less endorsement for preventing harm and unfairness in individuals with elevated psychopathic traits (Glenn et al., 2009a). Our recent study showed that unpleasantness plays a mediating role in psychopathic traits and moral judgment especially for the Harm and Fairness foundations (Ye et al., 2021). However, few studies have yet directly examined the underlying neural substrates of the relationship between psychopathic traits and concern with the moral foundations. Our current paper aims to explore the neural mechanism underlying the relationship between psychopathic traits and morality under the framework of MFT.

To date, much of our knowledge about the neural mechanism of the relationship between psychopathic traits and morality is from task-dependent fMRI studies, which associate blood oxygenation level-dependent (BOLD) signals with moral judgments for individuals with higher psychopathic traits. In particular, many of these studies revealed altered brain functions in brain regions supporting emotion processing, such as the amygdala. For example, individuals with elevated psychopathic traits show decreased activation in the amygdala during moral decision-making (Glenn et al., 2009b; Harenskia et al., 2014; Yoder et al., 2015). Youths with higher psychopathic traits show reduced functional connectivity between the amygdala and orbitofrontal

cortex (OFC) when making moral judgments (Marsh et al., 2011). In addition, male inmates with higher psychopathic traits demonstrate decreased functional connectivity between the amygdala and right temporoparietal junction when viewing morally bad scenarios (Yoder et al., 2015).

Task-independent resting-state fMRI (RS-fMRI) offers an appealing alternative to characterize the neural functions of individuals with mental health concerns (Philippi et al., 2015). RS-fMRI measures intrinsic brain functions by scanning participants while they maintain a relatively relaxed state in a scanner. Compared with task-fMRI, RS-fMRI measures have a better signal to noise ratio and have good reliability (Fox & Greicius, 2010). Recent evidence has shown altered resting-state architecture of functional brain organization associated with psychopathic traits. In particular, abnormal functional connectivity between limbic-paralimbic structures (e.g., insula, amygdala, and posterior cingulate cortex [PCC]) and prefrontal areas (e.g., ventromedial prefrontal cortex [vmPFC], dorsal medial prefrontal cortex [dmPFC], ventrolateral prefrontal cortex, and dorsolateral prefrontal cortex) have been shown to be related to elevated psychopathic traits (Contreras-Rodriguez et al., 2014; Motzkin et al., 2011). Overall, RS-fMRI findings also reveal altered functional connectivity between emotional-related brain regions (e.g., the amygdala) and other brain areas including the prefrontal areas for individuals with higher psychopathic traits (Blair, 2007; Contreras-Rodriguez et al., 2014; Espinoza et al., 2019; Motzkin et al., 2011). However, those RS-fMRI studies have provided little information about how resting-state functional connectivity between those regions of interest underlie the relationship of psychopathic traits to moral cognition. Especially, little is known about the direction of these connections (i.e., functional connectivity, FC) during moral cognition for people with elevated psychopathic traits. Finding out the direction

of the information transmission between brain regions might deepen our understanding of the neural mechanism underlying the moral cognition for people with elevated psychopathic traits. For example, given the atypical emotional processing widely associated with psychopathic traits, we might want to know whether it is because brain regions supporting emotional functions send or receive atypical inputs from other brain regions.

Effective connectivity (EC) provides an estimation of the directional relationship between brain regions. Therefore, information about the possible causal influence of one region on another can be inferred (Friston & Moran, 2013). Granger causality analysis (GCA) is a data-driven method for investigating the effective connectivity between recorded time series of brain regions without a prior specification of causal setting (Seth et al., 2015). Using this method might increase our knowledge about the atypical neural circuits associated with moral cognition for individuals with higher psychopathic traits in terms of causal relationships between brain regions without a prior hypothesis of the brain connectivity models.

In our study, we aimed to utilize a GCA approach to explore the intrinsic neural signatures for the relationship between psychopathic traits and concern with different moral foundations. We focused on brain regions that have been proved to be significantly associated with psychopathic traits in a recent meta-analysis including the amygdala, dmPFC, PCC, anterior cingulate cortex (ACC), OFC, and hippocampus (Deming & Koenigs, 2020). Given the essential role of emotion in the relationship between psychopathic traits and moral cognition (Glenn et al., 2009a; Patil, 2015; Ye et al., 2021), we expected that the EC from brain regions that are particularly related to emotional function (e.g., amygdala) to other brain regions might mediate the relationship between psychopathic traits and moral foundations, especially for the

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147 Harm and Fairness foundations. In other words, those brain areas supporting
148 emotional function might exert atypical influence on other brain regions during moral
149 cognition for individuals with elevated psychopathic traits. Additionally, We expected
150 our findings to be more pronounced for primary psychopathy than secondary
151 psychopathy as recently we found psychopathic traits are correlated with moral
152 judgments merely in primary psychopathy (Ye et al., 2021).

153 **METHOD**

154 **Participants**

155 Seventy-eight college students from local universities participated in this study. All
 156 the participants were right-handed and in healthy condition. No participants reported
 157 any history of neurological or psychiatric disorder. During the study, one participant
 158 failed to complete the questionnaires, five participants were detected to provide
 159 inappropriate answers in the bogus items in MFQ, and two participants had head
 160 motions exceeding 2° during scanning. These participants were excluded from further
 161 analyses, leaving a final sample of 70 participants (29 males; 22.71 ± 2.51 years old,
 162 range: 18–30 years old) ([Tab.1](#)). The study was approved by the Ethical Committee of
 163 Hangzhou Normal University. All the participants provided written informed consent
 164 in accordance with the Declaration of Helsinki and were compensated by cash.

165 **--- Insert Table 1 about here ---**

167 **Measures and Procedure**

168 *Measures*

169 *Levenson Self-Report Psychopathy Scale (LSRP)* Psychopathic traits were assessed
 170 with the LSRP which has been well validated in the community sample ([Levenson et](#)
 171 [al., 1995](#)). The scale consists of 26 items, each of which can be scored on a 4-point
 172 Likert scale ranging from 1 (strongly disagree) to 4 (strongly agree). The
 173 questionnaire includes two separate subtypes of psychopathy (i.e., primary
 174 psychopathy and secondary psychopathy). Primary psychopathy corresponds to
 175 Factor 1 (interpersonal/affective traits) whereas secondary psychopathy corresponds
 176 to Factor 2 (lifestyle/antisocial traits) of The Psychopathy Checklist-Revised which is
 177 a structured clinical assessment. The higher scores on the scale indicate higher

178 psychopathic traits (Lynam et al., 1999). The Chinese version of the LSRP has been
179 proved to have good reliability (M.-C. Wang et al., 2018). The Cronbach's alpha was
180 0.76 (total psychopathic traits score [T-PTS]), 0.72 (primary psychopathic traits score
181 [P-PTS]) and 0.59 (secondary psychopathic traits score [S-PTS]) in the present
182 sample.

183 *Moral Foundation Questionnaire (MFQ)* The concern with different moral
184 foundations were evaluated by the MFQ, which consists of 32 items (Graham et al.,
185 2009). The scale contains two sections. The first section measures the moral relevance
186 of different moral considerations on a six-point Likert scale ranging from 0 (not at all
187 relevant) to 5 (extremely relevant) while the second section measures the degree to
188 which participants agreed or disagreed with stated moral views on a six-point Likert
189 scale ranging from 0 (strongly disagree) to 5 (strongly agree). The scores of five
190 moral foundations (i.e., Harm, Fairness, Loyalty, Authority, and Purity) were
191 calculated respectively, with higher scores indicating higher concern of the
192 corresponding moral foundation. The questionnaire has been well-validated in
193 Chinese sample (Du, 2019; R. Wang et al., 2019). The Cronbach's alpha of subscales
194 was 0.41 (Harm), 0.58 (Fairness), 0.53 (Loyalty), 0.61(Authority) and 0.62 (Purity) in
195 the present sample.

196 *Procedure*

197 Participants completed two questionnaires after undergoing task-free fMRI. The order
198 of the two questionnaires were counterbalanced among participants.

199

200 **Behavioral data analyses**

201 The statistical analyses for questionnaire measures were performed using SPSS
202 Version 23.0 (IBM Corp. Released 2015) with an alpha value of $p < 0.05$ (two tailed).

10

203 Linear regression analyses were performed to examine whether total LSRP score,
204 primary psychopathy, and secondary psychopathy could predict concern with the five
205 moral foundations after controlling the demographic regressors (i.e., age and gender).

206

207 **Imaging acquisition**

208 All MRI data were acquired at the Center for Cognition and Brain Disorders of
209 Hangzhou Normal University using a 3T MRI scanner (GE Discovery 750 MRI,
210 General Electric, Milwaukee, WI, USA). The participants were scanned for 8 minutes
211 and instructed to keep their eyes closed and remain awake without performing any
212 systematic thinking. Head motion was minimized using foam padding and restraint.
213 The imaging parameters of the EPI sequence were as follows: repetition time (TR) =
214 2000ms; interleaved 43 slices; echo time (TE) = 30 ms; thickness = 3.2mm; flip angle
215 = 90°; field of view (FOV) = 220 × 220 mm²; and matrix size = 64 × 64. Each fMRI
216 scan included 240 imaging volumes. In addition, a high-resolution 3D T1-weighted
217 anatomical image was also acquired using a magnetization prepared gradient echo
218 (MP-RAGE) sequence with following imaging parameters: 176 sagittal slices; TR =
219 8,100ms; slice thickness = 1 mm; TE = 3.1ms; flip angle = 8°; FOV = 250 × 250 mm.

220

221 **Preprocessing**

222 The neuroimaging data were preprocessed using the DPABI software package based
223 on SPM12 (Yan et al., 2016). The first 10 volumes of the functional images were
224 discarded to eliminate the non-equilibrium effects of magnetization. Then, slice
225 timing and head motion correction were applied. Corrected functional images were
226 registered to the corresponding T1-weighted anatomical image and spatially
227 transformed to the standard MNI space with 3 × 3 × 3 mm³ voxels. A band-pass

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temporal filtering (0.01–0.1 Hz) was subsequently applied to the time series to reduce the effect of low-frequency drifts and high-frequency physiological noise. Next, the images were spatially smoothed using an isotropic Gaussian kernel with 4mm full width at half maximum to decrease spatial noise. Finally, the linear trends of time courses were removed, and three common nuisance variables including 24 head-motion parameters and averaged signals from the cerebrospinal fluid and white matter were regressed out.

Selection of the regions of interest

To access the EC of the regions that are most relevant to psychopathic traits, a priori seed regions of interest (ROIs) were selected that have been identified from a meta-analysis (Deming & Koenigs, 2020): anterior cingulate cortex (ACC), dorsomedial prefrontal cortex (dmPFC), inferior frontal gyrus (IFG), posterior orbitofrontal cortex (OFC), amygdala, hippocampus, and calcarine (Tab.2). Each ROI was centered on the coordinates in MNI space provided by the meta-analysis and include a radius sphere of 5 mm (Fig.1b).

--- Insert Table 2 and Figure 1 about here ---

Granger causality analysis

Bivariate coefficient-based GCAs were performed to examine EC among ROIs and each voxel of the whole brain using the REST v1.8 toolbox (Song et al., 2011; Zang et al., 2012). This GCA approach assumes that if including past values of a BOLD time series x lead to better prediction of the current value of time series y , then series x causes series y (Roebroeck et al., 2005). Here, the BOLD time series of each ROI was defined as the seed time series x , and the time series of voxels within the whole brain

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253 were defined as the time series y . The positive value of EC from series x to series y
 254 indicates an excitatory effect that series x imposes on series y , whereas the negative
 255 value was interpreted as an inhibitory effect (Zang et al., 2012). Finally, Fisher's r -to-
 256 z transformations were implemented (Fig.1c).

257

258 **Partial correlation analyses**

259 Voxel-wise EC for all seed ROIs significantly associated with psychopathic traits (T-
 260 PTS, P-PTS, and S-PTS) were examined by using partial correlation analyses with
 261 age and gender as covariates (Fig.1d). To correct for multiple comparisons, family-
 262 wise error (FWE) correction with Gaussian random field theory was applied, in which
 263 the voxel threshold was set to $p < 0.001$ and the cluster threshold was set to $p < 0.05$
 264 with two tails. Next, the relationship between the neuroimaging findings (i.e., EC
 265 significantly related to psychopathic traits) and concern with the five moral
 266 foundations was examined (Fig.1e). The values of EC that was significantly related to
 267 psychopathic traits were extracted. Then, Pearson correlation analyses were further
 268 conducted to examine the relationship between these EC values and concern with the
 269 five moral foundations with age and gender as covariates. Here, Bonferroni correction
 270 for multiple comparisons ($n = 65$) was applied to control the false-positive results.

271

272 **Mediation analyses**

273 For the EC that was significantly associated with both psychopathic traits and the
 274 concern with the five foundations, mediation analyses were conducted to examine
 275 whether relationship between psychopathic traits and moral concern was mediated by
 276 the EC (Fig.1f). The mediation analyses were conducted by applying Bootstrapping
 277 PROCESS for SPSS with age and gender as covariates. The Bootstrap samples were

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278 set as 5,000, and the confidence level (CI) for confidence intervals was set as 95%.

279 The CI which does not include zero suggests a significant mediation role in the

280 relationship between psychopathic traits and the concern with the five foundations.

281 **RESULTS**

282 **Relationship between psychopathic traits and five moral foundations**

283 The relationship between psychopathic traits and concerns with the moral foundations
284 were examined by establishing linear regression models. The results showed that
285 concern with the Harm foundation was significantly predicted by T-PTS ($\beta = -0.461$, p
286 < 0.001) and P-PTS ($\beta = -0.498$, $p < 0.001$). However, psychopathic traits did not
287 predict concern with the other four foundations (i.e., Fairness, Loyalty, Authority and
288 Purity) (**Tab. 3**).

289 **--- Insert Table 3 about here ---**

290 **Relationship between psychopathic traits and EC**

291 Partial correlation analyses were conducted to examine the voxel-wise EC that were
292 significantly associated with psychopathic traits. The results showed that T-PTS was
293 significantly related to the EC from the posterior insula to the amygdala, from the
294 dmPFC to the middle temporal gyrus and precentral gyrus, and from the PCC to the
295 dmPFC (**Fig.2**). P-PTS was significantly correlated with the EC from the posterior
296 insula and supramarginal gyrus to the amygdala, from the dmPFC to the precentral
297 gyrus and IPL, from the PCC to the dmPFC, and from the ACC to the middle
298 temporal gyrus (**Fig.3**). However, no EC was found to be significant correlated with
299 S-PTS. The detailed results for the relationship between the EC and psychopathic
300 traits are shown in Table 4.

301 **--- Insert Figures 2, 3, and 4 about here ---**

302 **Relationship between concern with moral foundations and EC that were** 303 **significantly related to psychopathic traits**

304 Partial correlation analyses were further conducted between the EC that was
305 significantly associated with psychopathic traits and concern with the Harm

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306 foundations. For the EC that was significantly correlated with T-PTS, a positive
307 correlation between the EC from the posterior insula to the amygdala and the Harm
308 foundation and a negative correlation between the EC from the dmPFC to the
309 precentral gyrus and the Harm foundation was found. For the EC that was
310 significantly correlated with P-PTS, a positive correlation between the EC from the
311 posterior insula to the amygdala and the Harm foundation, and a negative correlation
312 between the EC from the amygdala to the supramarginal gyrus and the Harm
313 foundation were found. However, no correlations were found between the other four
314 foundations and the EC that was significantly related to psychopathic traits (see **Tab.**
315 **4**).

316

317 **Mediation analysis**

318 For EC significantly correlated with both psychopathic traits and concern with the
319 Harm foundation (i.e., EC from the posterior insula to the amygdala, and from the
320 dmPFC to the precentral gyrus), mediation analyses were further performed to
321 investigate whether the EC mediated the relationship between psychopathic traits and
322 the concern with the Harm foundation. The indirect effect of T-PTS through the EC
323 from the posterior insula to the amygdala (95% CI = [-0.150, -0.003]) on the Harm
324 foundation was significant. The direct effect of T-PTS on the Harm foundation was
325 still significant when the EC was included as a mediator (95%CI = [-0.268, -0.025]),
326 indicating that the EC from the posterior insula to the amygdala partially mediated the
327 relationship between T-PTS and concern with the Harm foundation. No mediation
328 effect of T-PTS through the EC from the dmPFC to the precentral gyrus on the Harm
329 foundation was observed (95%CI = [-0.128, 0.169]) (**Fig.4**).

330

--- Insert Figure 4 about here ---

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331 Similarly, the indirect effect of P-PTS through the EC from the posterior insula
 332 to amygdala (95%CI = [-0.400, -0.041]) on the Harm foundation was significant, but
 333 the indirect effect of P-PTS through EC from the amygdala to the supramarginal
 334 gyrus (95%CI = [-0.163, 0.020]) was not significant, Moreover, the direct effect of P-
 335 PTS on the Harm foundation was still significant when the EC was included as a
 336 mediator (95%CI = [-0.249, -0.001]), indicating that the EC from the posterior insula
 337 to the amygdala partially mediated the relationship between P-PTS and concern with
 338 the Harm foundation (Fig. 5).

339 --- Insert Figure 5 about here --

340 **DISCUSSION**

341 This study combined self-report questionnaires with RS-fMRI EC to reveal the
 342 intrinsic neuropsychological mechanism of the relationship between psychopathic
 343 traits and concern with different moral foundations. At the behavior level, we found
 344 that T-PTS and P-PTS predicted moral concern with the Harm foundation, but not the
 345 other four foundations. At the neural level, we found that reduced EC from the
 346 posterior insula to the amygdala was associated with higher psychopathic traits and
 347 greater concern for the harm foundation. Furthermore, the EC from the posterior
 348 insula to the amygdala partially mediated the relationship between T-PTS/P-PTS and
 349 concern with the Harm foundation. Our findings provided the first neural evidence for
 350 less concern with the harm foundation for individuals with higher psychopathic traits
 351 and deepened our understanding of the underlying mechanism of atypical moral
 352 cognition associated with psychopathic traits.

353 Our behavioral results demonstrated that T-PTS and P-PTS significantly
 354 predicted moral concern with Harm foundation only. This is consistent with previous
 355 studies which reported significant association between psychopathic traits and
 356 different moral foundations, with the effects being most pronounced for the Harm
 357 foundation (Aharoni et al., 2011; Gay et al., 2018; Glenn et al., 2009a; Marshall et al.,
 358 2018). Perception of harm is intuitive, forming the fundamental basis of moral
 359 judgment (Haidt & Joseph, 2004; Schein & Gray, 2017). A systematic review
 360 suggested that psychopathy is primarily associated with compromised care-based
 361 morality involving moral reasoning about harmful actions to others (Blair, 2007).
 362 Here, we provided more evidence that psychopathic traits are more related to harm-
 363 based moral cognition than other types of moral cognition.

364 Our neural results showed that decreased EC from the posterior insula to the

365 amygdala was associated with higher psychopathic traits. The amygdala and insula
 366 are core components of the salience network (SN), a large-scale brain network widely
 367 recognized to be involved in detection and integration of emotional and sensory
 368 stimuli (Geng et al., 2016). Both of the two regions take a crucial role in saliency
 369 processing, attention capturing and identification of emotional significance of the
 370 stimulus (Calder et al., 2001; Menon & Uddin, 2010; Phillips et al., 2003). Since
 371 dysfunctional emotional responses are characteristic features of individuals with
 372 higher psychopathic traits, atypical neural activity in the amygdala and insula is very
 373 likely to be associated with psychopathic traits (Blair, 2013; Dolan & Fullam, 2009;
 374 Ermer et al., 2012; Santana, 2016; Yang et al., 2009). For example, a systematic
 375 review suggested that brain regions implicated in psychopathic traits include the
 376 amygdala, insula, anterior and posterior cingulate, etc. (Santana, 2016). Individuals
 377 with higher psychopathic traits show reduced amygdala and insula volume (Ermer et
 378 al., 2012; Yang et al., 2009), as well as decreased neural activity in the amygdala and
 379 insula (Blair, 2013; Dolan & Fullam, 2009). Furthermore, individuals with higher
 380 psychopathic traits show altered anatomical and functional connectivity between the
 381 two regions and other brain areas, and between the two regions themselves during
 382 socio-moral decision making (Fumagalli & Priori, 2012; Han et al., 2016; Shenhav &
 383 Greene, 2014).

384 The insula is anatomically and functionally connected with the amygdala
 385 (Augustine, 1985, 1996; Gasquoin, 2014; Sethi et al., 2018; J. L. Stein et al., 2007).
 386 This pathway constitutes a part of the network associated with salience and emotion
 387 processing (Baur et al., 2013; Geng et al., 2016). The insula has been commonly
 388 recognized to translate bodily state information into emotional feelings (Dennis et al.,
 389 2011; Uddin, 2014; Yu et al., 2015). The interoceptive signals arrived in the posterior

insula before being evaluated and represented in the anterior insula (Craig & Craig, 2009; Straube & Miltner, 2011). The right posterior insula is considered to be especially involved in the awareness of one's own bodily states. When people pay more attention to their own emotions, the activities of the primary somatosensory cortex as well as the posterior insula increase (Straube & Miltner, 2011). The amygdala receives inputs of various sensory and emotional information from other brain regions (Diano et al., 2017; Hofmann & Straube, 2019) including the posterior insula. Evidence showed that resting-state connectivity between the amygdala and the posterior insula decreased with emotional dysregulation (Bebko et al., 2015). The amygdala may detect and integrate the bodily state information transmitted from the posterior insula to support adaptive emotional responses (Babaev et al., 2018; Bebko et al., 2015; Stein et al., 2007). We argued that as the EC from the posterior insula to the amygdala decreases, the capacity to recognize and integrate bodily state information into emotional responses might weaken for individuals with higher psychopathic traits.

Furthermore, we found that the EC from the posterior insula to the amygdala partially mediated the relationship between psychopathic traits and the concern with the Harm foundation. In conjunction with previous behavioral findings that emotion responses serve as a mediator in the relationship between psychopathic traits and morality (Glenn et al., 2009; Patil, 2015; Ye et al., 2021), the results here suggested that weakened capacity to integrate bodily-state information to emotional responses in individuals with elevated psychopathic traits in response to moral contexts accounts for their emotional shallowness, which partially contributes their atypical moral cognition. Importantly, the significant relationship between psychopathic traits and morality as well as the mediating role of the posterior insula-to-amygdala connectivity

in the relationship was only observed in T-PTS and P-PTS, but not S-PTS. These results concur with previous findings that only primary psychopathy is able to predict moral judgments in the contexts of sacrificial moral dilemmas (Takamatsu & Takai, 2019) and every-day moral scenarios (Ye et al., 2021). Primary psychopathy covers interpersonal and affective features, whereas secondary psychopathy represents aggressive and antisocial lifestyles (Hare, 1991). The primary psychopathic subtype normally demonstrates significantly lower anxiety than the secondary subtype (Lee & Salekin, 2010; Skeem et al., 2007; Vaillancourt & Brittain, 2019). In addition, reduced amygdala and insula activity in response to fear stimuli is merely associated with the primary psychopathy (Sethi et al., 2018). Overall, our findings supported that primary psychopathy contributes remarkably more than the secondary psychopathy to the atypical moral cognition and the neural underpinnings of the relationship of the two subtypes of psychopathic traits to moral cognition might differ significantly.

It is noteworthy that the aforementioned neural finding (i.e., the posterior insula-amygdala EC) was restricted to the right hemisphere which is more frequently involved in the processing of all kinds of emotions, especially negative emotions (Bowu et al., 1988; Gainotti, 2019; Killgore & Yurgelun-Todd, 2007). For example, increased activations were observed in emotion-related brain regions anchored in the right hemisphere (e.g., the right vmPFC and right amygdala) during a facial emotion perception task, especially in the case of facial cues with negative emotions (Killgore & Yurgelun-Todd, 2007). Thus, the EC from the posterior insula to the amygdala related to psychopathic traits and morality was only found in the right hemisphere may be due to the lateralized processing of negative emotion.

Additionally, we found that the EC from the dmPFC to the precentral gyrus was significantly correlated with T-PTS and P-PTS. Increased EC from the dmPFC to the

440 precentral gyrus was associated with higher psychopathic traits. The dmPFC
 441 contributes to cognitive control and goal-oriented action selection ([Ridderinkhof et](#)
 442 [al., 2004](#); [Venkatraman et al., 2009](#)) whereas the precentral gyrus is responsible for
 443 the control of voluntary motor movement ([Loukas et al., 2011](#)). The altered EC from
 444 the dmPFC to the precentral gyrus might be linked to poorer behavioral control of
 445 individuals with higher psychopathic traits compared to those with lower
 446 psychopathic traits who are more capable of appropriately taking goal-oriented
 447 actions. However, we did not find any mediating effect of the EC from the dmPFC to
 448 the precentral gyrus on the relationship between psychopathic traits and morality.
 449 Therefore, the increased communication from the dmPFC to the precentral gyrus
 450 might be part of the intrinsic neural characteristics for psychopathic traits but not the
 451 potential neural mechanism for how psychopathic traits were linked to morality.

452 Several limitations of this study are noteworthy. First, only college students were
 453 included as the participants and the sample size was relatively modest. Replication in
 454 a larger community sample is needed in the future to enhance the generalizability of
 455 our findings. Second, some items in the MFQ items seem rather abstract and obscure
 456 for participants, leading to relatively low validity and reliability of the scale. More
 457 accessible measures for morality (e.g., daily moral scenarios) should be utilized in the
 458 future to improve the reliability and especially the external validity of the
 459 measurement ([Clifford et al., 2015](#); [Ye et al., 2021](#)). Third, ROIs used in the study
 460 were from a meta-analysis, which may bias the results as we may overlook other
 461 important brain areas (vmPFC, posterior cingulate, and superior temporal gyrus) that
 462 are related to psychopathic traits. In addition, the repetition time of RS-fMRI in our
 463 study was 2 s which is much slower than the neuron reaction time. However, many
 464 researchers believe that even in the case of using long TRs to collect fMRI data, GCA

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465 still estimates the time-directional influences ([Liao et al., 2010](#) ; [Rajan et al., 2019](#)).
 466 Finally, future studies should also examine the relationship between psychopathic
 467 traits and moral concern in the Liberty foundation which was recently validated as a
 468 new moral foundation ([Graham et al., 2018](#)).

469 Taken together, the present study revealed the underlying neuropsychological
 470 signatures of the relationship between psychopathic traits and concern with different
 471 moral foundations. Our findings demonstrated that T-PTS and P-PTS predicted
 472 concern with the Harm foundation. Importantly, higher psychopathic traits were
 473 associated with reduced EC from the posterior insula to the amygdala, which partially
 474 mediated the relationship between psychopathic traits and concern with the Harm
 475 foundation. These findings provided new evidence for the special role of psychopathic
 476 traits in concern with different foundations and shed new light on the
 477 neuropsychological mechanisms underlying the relationship between psychopathic
 478 traits and morality. This study increases our knowledge about the atypical neural
 479 circuits associated with moral cognition for higher-psychopathic-trait individuals in
 480 terms of effective connectivity between brain regions and may have some
 481 implications for early prevention of individuals with higher psychopathic traits from
 482 committing serious transgressions.

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767 Table Legends

768 **Table 1. Demographic information.**

	Male (N=29)		Female (N=41)		<i>p</i> -value
	Mean	SD	Mean	SD	
Age (years)	23.52	2.86	22.15	2.08	
T-PTS	52.34	7.41	53.68	7.70	0.469
P-PTS	32.69	5.57	33.00	5.10	0.810
S-PTS	19.66	3.15	20.68	3.56	0.217
Harm foundation	19.10	3.93	20.49	3.24	0.112
Fairness foundation	19.72	4.57	20.56	3.10	0.363
Loyalty foundation	18.24	3.47	20.17	3.71	0.031 [*]
Authority foundation	16.21	4.72	17.68	3.54	0.139
Purity foundation	15.38	4.59	16.63	4.02	0.229

769 SD: standard deviation; LSRP: the Levenson Self-Report Psychopathy Scale; T-TPS: total
 770 psychopathic traits score; P-PTS: primary psychopathic traits score; S-PTS: secondary
 771 psychopathic traits score.

772 ^{*}: $p < 0.05$

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Table 2. Seeds selected to evaluate effective connectivity.

Seed regions	Hemi.	MNI coordinates		
		x	y	z
Anterior cingulate cortex	L	-6	32	22
Dorsomedial prefrontal cortex 1	L/R	-2	56	28
Dorsomedial prefrontal cortex 2	L/R	-2	50	34
Dorsomedial prefrontal cortex 3	L/R	2	44	32
Inferior frontal gyrus	R	40	40	-8
Posterior orbitofrontal cortex	R	26	8	-16
Amygdala	R	30	4	-20
Hippocampus 1	R	24	-36	2
Hippocampus 2	R	30	-40	-4
Calcarine	R	12	-70	16

L: left; R: right

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Table 3. Regression coefficients for the T-PTS, P-PTS, S-PTS, and concern with five moral foundations.

	Regression coefficient		
	T-PTS	P-PTS	S-PTS
Harm	-0.461***	-0.498***	-0.258
Fairness	-0.174	-0.243	-0.011
Loyalty	-0.072	-0.036	-0.107
Authority	-0.066	-0.079	-0.024
Purity	-0.226	-0.156	-0.266

*** Bonferroni-corrected $p < 0.001$, $n=15$; T-PTS: total psychopathic traits score; P-PTS: primary psychopathic traits score; S-PTS: secondary psychopathic traits score.

Table 4. The Effective connectivity associated with psychopathic traits and their relationship to moral concern with moral foundations.

Seed regions	Direction	Brain regions	MNI coordinate			Peak Intensity	Cluster Size ^a	r-value				
			x	y	z			Harm	Fairness	Loyalty	Authority	Sanctions
T-PTS												
Dorsomedial prefrontal cortex 1	Output	Middle temporal gyrus	-57	-66	-3	0.484	47	-0.130	-0.093	0.132	-0.013	-0.117
Dorsomedial prefrontal cortex 2	Input	Posterior cingulate cortex	-3	-42	24	0.446	28	-0.260	-0.277	0.158	0.051	-0.011
Dorsomedial prefrontal cortex 3	Input	Posterior cingulate cortex	6	-42	12	0.529	144	-0.248	-0.063	0.057	-0.037	-0.154
Dorsomedial prefrontal cortex 3	Output	Precentral gyrus	48	0	45	0.538	59	-0.405*	-0.178	-0.136	-0.075	-0.261
Amygdala	Input	Posterior insula	39	-9	18	-0.507	27	0.414*	0.241	0.048	0.047	0.205
P-PTS												
Anterior cingulate cortex	Output	Middle temporal gyrus	-45	-75	15	0.447	34	-0.256	-0.319	0.032	-0.107	-0.085
Dorsomedial prefrontal cortex 1	Output	Precentral gyrus	45	0	45	0.514	46	-0.239	-0.229	-0.001	0.100	-0.121
Dorsomedial prefrontal cortex 2	Input	Posterior cingulate cortex	-3	-45	18	0.453	34	-0.160	-0.190	0.173	0.030	0.023
Dorsomedial prefrontal cortex 3	Input	Posterior cingulate cortex	3	-45	15	0.547	126	-0.258	-0.075	0.050	-0.049	-0.152
Dorsomedial prefrontal cortex 3	Output	Inferior parietal lobe	39	-42	57	0.496	37	-0.188	-0.044	-0.091	-0.233	-0.179
Dorsomedial prefrontal cortex 3	Output	Precentral gyrus	48	0	45	0.583	84	-0.375	-0.221	-0.153	-0.055	-0.262
Amygdala	Input	Posterior insula	39	-9	21	-0.542	78	0.451*	0.225	0.036	0.090	0.230
Amygdala	Input	Supramarginal gyrus	60	-42	39	0.498	27	-0.395*	-0.137	0.131	-0.149	-0.163

a: Number of voxels. FWE ($p < 0.05$) with voxel- $p < 0.001$. Voxel size = $3 \times 3 \times 3$.

T-PTS: total psychopathic traits score; P-PTS: primary psychopathic traits score.

*: Bonferroni-corrected $p < 0.05$, $n = 65$.

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Figure Legends

Figure 1. Workflow of the neuroimaging data analyses. First, preprocessed rs-fMRI data were used to calculate voxel-wise EC based on ten predefined ROIs (subplot a, b, and c). Then, partial correlation analyses were performed between EC and scores on psychopathic traits (i.e. T-PTS, P-PTS, and S-PTS) (subplot d). Next, partial correlation analyses were performed between EC that is significantly related to psychopathic traits and concerns with moral foundations (subplot e). Finally, mediation analyses were conducted to examine the mediation role of these EC in the relationship between psychopathic traits and concern with moral foundations (subplot f). T-PTS: total psychopathic traits score; P-PTS: primary psychopathic traits score; S-

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PTS: secondary psychopathic traits score.

Figure 2. EC that is significantly related to T-PTS.

By conducting partial correlation analyses, the EC from the dmPFC to the MTG and PrG, from the PCC to the dmPFC, and from the PI to the amygdala were found to be significantly related to T-PTS. The red arrow refers to a positive association between EC and T-PTS while the blue arrow refers to a negative association between EC and T-PTS. EC: effective connectivity; MTG: middle temporal gyrus; PCC: posterior cingulate cortex; PrG: precentral gyrus; PI: posterior insula; dmPFC: dorsomedial prefrontal cortex; T-PTS: total psychopathic traits score.

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Figure 3. EC that is significantly related to P-PTS.

By conducting partial correlation analyses, EC from the ACC to the MTG, from the dmPFC to the PrG and IPL, from the PCC to the dmPFC, and from the PI and SMG to the amygdala were found to be significantly related to P-PTS. The red arrow refers to a positive association between EC and P-PTS while the blue arrow refers to a negative association between EC and P-PTS. EC: effective connectivity; MTG: middle temporal gyrus; PCC: posterior cingulate cortex; PrG: precentral gyrus; PI: posterior insula; IPL: inferior parietal lobe; SMG: supramarginal cortex; ACC: anterior cingulate cortex; dmPFC: dorsomedial prefrontal cortex; P-PTS: primary psychopathic traits score.

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Figure 4. Correlation and mediation analyses (T-PTS).

(a) EC from the insula to the amygdala was negatively correlated with T-PTS. (b) EC from the posterior insula to the amygdala was positively associated with moral concern with the Harm foundation. (c) EC from the insula to the amygdala partially mediated the association between T-PTS and moral concern with the Harm foundation. EC: effective connectivity; PI: posterior insula; PI_R: right posterior insula; Amygdala_R: right amygdala; T-PTS: total psychopathic traits score.

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Figure 5. Correlation and mediation analyses (P-PTS).

(a) EC from the insula to the amygdala was negatively correlated with P-PTS. (b) EC from the insula to the amygdala was positively associated with concern with the Harm foundation. (c) EC from the insula to the amygdala partially mediated the association between P-PTS and concern with the Harm foundation. EC: effective connectivity; PI: posterior insula; PI_R: right posterior insula; Amygdala_R: right amygdala; P-PTS: primary psychopathic traits score.

(a) Preprocessed fMRI data

(b) ROI definition

(c) Voxel-wise GCA

Calculated the correlation between the voxel-wise EC for all seed ROIs and psychopathic traits

(d) EC that is related to psychopathic traits

(e) EC that is related to moral foundations

Calculated the correlation between the EC that is related to psychopathic traits and moral foundations

(f) The mediation model

(a) **(b)** **(c)**