

Neural signatures underlying the effect of social structure on empathy and altruistic behaviors

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ABSTRACT

Humans inhabit complex social networks, monitoring social structures that encompass both direct and indirect relationships. However, previous research primarily focused on direct relationships, leaving the neural basis of how social structure influences socioemotional processes understudied. This study addressed this gap by investigating the neural pathways underlying the influence of social structure on empathy and altruistic behaviors. During fMRI scanning, participants viewed painful or non-painful stimulation to innocent strangers who shared preferences with targets who had either treated participants fairly or unfairly. Afterwards, participants rated the pain experienced by these innocents and shared money with other innocents. Participants showed reduced empathic and altruistic responses toward innocents resembling unfair (vs. fair) targets, accompanied by heightened activation in regions crucial for emotion regulation and mentalizing, such as the lateral and medial prefrontal cortex. Furthermore, whole-brain and local neural patterns in the anterior insula and premotor cortex robustly discriminated painful (but not non-painful) stimulation of different innocents, suggesting that social structure altered emotional and sensorimotor aspects of empathy. These alterations might be driven by top-down regulation, as indicated by heightened functional connectivity between the lateral prefrontal cortex and sensorimotor areas, as well as between the anterior insula and subgenual anterior cingulate cortex when witnessing the pain of innocents resembling fair (vs. unfair) targets. Together, our work is the first to uncover the neural underpinnings through which human empathy and altruistic behaviors are shaped by social structure beyond direct self-other relationships.

1. Introduction

Social structure, defined as the organized pattern of both direct and indirect ties among individuals within a social network, shapes how we perceive and interact with others (Gershman and Cikara, 2020; Parkinson and Du, 2020; Weaverdyck and Parkinson, 2018). Our

connections therefore extend beyond immediate, dyadic interactions. For example, one might feel an affinity toward a stranger simply because they share a hometown with a close friend, or harbor distrust toward members of another community due to intergroup conflicts, despite lacking any personal contact. Rather than tracking only visible, direct relationships, humans continuously infer these broader social structures

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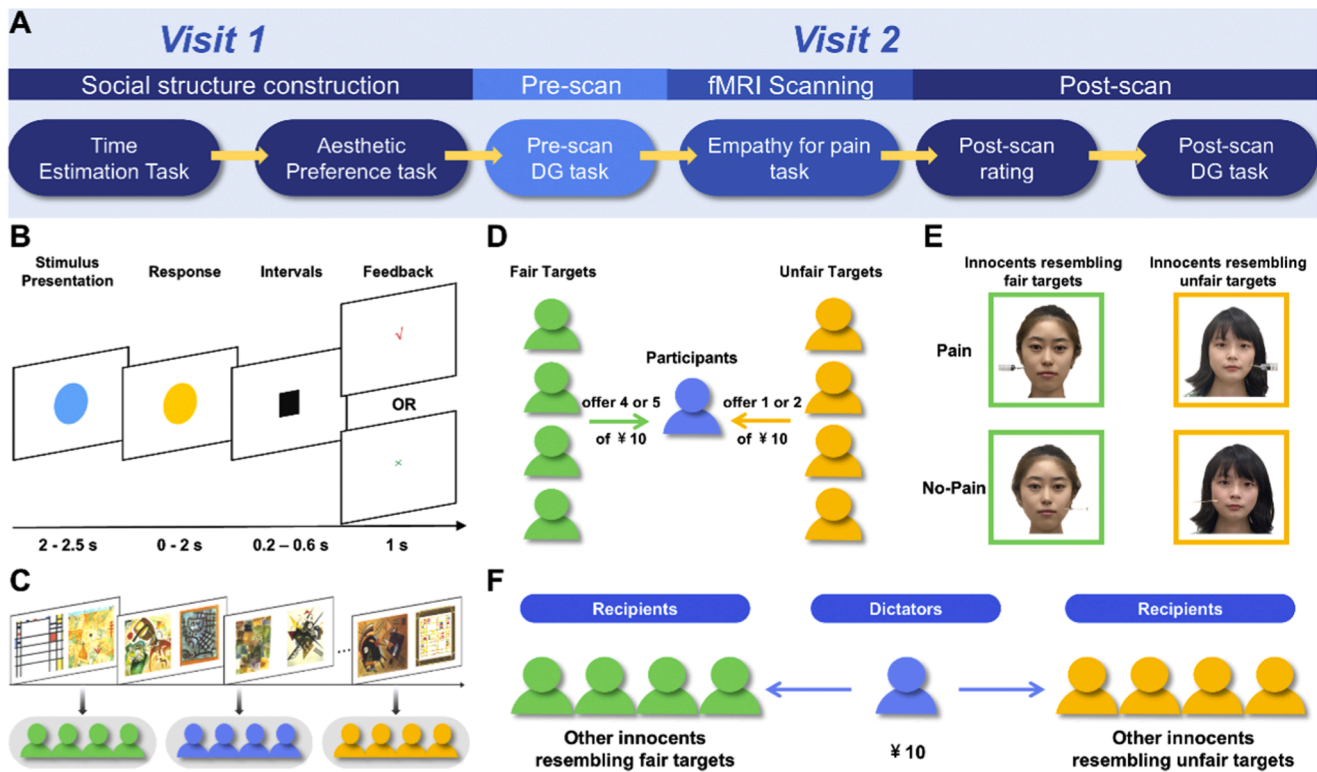


Fig. 1. Task design and experimental procedure. **A** The experimental procedure. **B** The timeline of the time estimation task. On each trial, a blue circle was presented for 2–2.5 s, and participants were instructed to estimate the duration of 1 s of the color change within 2 s. Feedback was presented for 1 s after an interval of 0.2–0.6 s. **C** The procedure of the aesthetic preference task. Pictures of three different styles were shown to participants in pairs, and then participants obtained their aesthetic preference represented by colors: green, blue, and yellow. **D** The experimental settings in the pre-scan Dictator Game. Participants (denoted by color blue) observed and received fair allocations from dictators (i.e., fair targets) with one aesthetic preference (denoted by color green) while unfair allocations from dictators (i.e., unfair targets) with another aesthetic preference (denoted by color yellow). **E** Illustration of innocents resembling fair targets (left) or unfair targets (right) receiving pain and non-painful stimulation. The color of the frame outside the photographs indicated the aesthetic preference information. **F** The post-scan Dictator Game. Participants acted as a dictator and decided how to allocate 10 yuan between themselves and the other dissimilar innocents. DG, Dictator Game. Note: the photographs displayed in the figure were not employed in the experiment but were only used for illustration purposes.

to navigate complex social environments (Arzy and Kaplan, 2022; Gershman and Cikara, 2020; Lau et al., 2020; Parkinson et al., 2017; Radulescu et al., 2021). Typically, individuals expand their social networks based on existing ties, preferring to cooperate with friends of friends over the friends of enemies (Brent, 2015; Sehl et al., 2023). Additionally, people retaliate against out-group innocents closely linked to those who attacked their in-group, even if they were not directly involved (Cushman et al., 2012; Han et al., 2020; Sjöström and Gollwitzer, 2015). Similarly, individuals may punish in-group members who act generously toward hostile out-group members (Chiang, 2020). Although social structures significantly shape diverse social interactions, prior research primarily concentrated on direct relationships (Weaverdyck and Parkinson, 2018). Thus, the neural mechanisms driving the influence of social structures on the socioemotional processes vital for social interactions are still not well understood.

Empathy is a fundamental element of human social functioning, broadly referring to the capacity to understand and share the emotional states of others (Schurz et al., 2021). Rather than a unitary construct, empathy comprises multiple interacting components, including affective empathy (emotional sharing), cognitive empathy (perspective-taking or mentalizing), personal distress (self-oriented discomfort in response to another's suffering), and compassion (other-oriented concern and motivation to help) (Decety et al., 2016; Decety and Jackson, 2004; Singer and Klimecki, 2014; Weisz and Zaki, 2018; Zaki and Ochsner, 2012). Among these components, the present study focuses on affective empathy, the embodied sharing of another's emotional state. Affective empathy is proposed to arise from shared neural representations between first-person and vicarious experiences of

emotion, such that observing another's emotional state engages motor, autonomic, and somatic responses in the observer (Jackson et al., 2006; Jin et al., 2018; Preston and De Waal, 2002; Ren et al., 2022). Indeed, brain regions associated with emotional and sensorimotor processing—such as the anterior insula (AI), anterior cingulate cortex (ACC), and somatosensory/motor cortices—are consistently activated during both direct and vicarious experiences of pain (Keysers et al., 2010; Lamm et al., 2011; Meng et al., 2013; Tu et al., 2023).

However, empathy is not merely an automatic response, it is flexible and malleable by social relations (Azevedo et al., 2013; Cheng et al., 2010; Cikara et al., 2011; Feng et al., 2016; Hein et al., 2016, 2010; Meyer et al., 2014; Singer et al., 2006). For example, during the COVID-19 pandemic, individuals often empathized with infected friends but held "deserved" sentiments towards innocent strangers tied to virus-related groups. The modulations of social relations on empathic responses could be afforded by top-down regulations, closely resembling those engaged by emotional regulation (Engen and Singer, 2013). Particularly, when faced with pain of strangers (vs. close others), brain regions linked to social cognition and cognitive control, like the dorsomedial prefrontal cortex (dmPFC), temporoparietal junction (TPJ), and lateral PFC (IPFC), show increased activity (Cheng et al., 2010; Lamm et al., 2010; Meyer et al., 2012). This implicates the deployment of multiple emotional regulation strategies to adjust empathic responses according to self-other relations, likely by modulating pain-related affective and sensorimotor processing (Decety and Meyer, 2008; Morawetz et al., 2020; Weisz and Zaki, 2018). Despite extensive research on the influence of direct relations on empathy, the neuropsychological processes supporting the role of social structure in empathy have yet to

be unveiled.

Here, we examined the neural substrates of how social structure modulates empathic and related altruistic responses (Fig. 1), combining functional MRI (fMRI) technique with local/whole-brain multivariate pattern analysis (MVPA) and functional connectivity analysis. An aesthetic preference task was first employed to construct social relations among participants in the experiment based on similarity in the aesthetic preference (Fig. 1C). Participants then experienced fair or unfair treatment by two types of targets with distinct aesthetic preferences (Fig. 1D). During fMRI scanning, they were exposed to painful or non-painful stimulation to innocent strangers who had no direct interaction with participants but shared aesthetic preferences with one type of targets (Fig. 1E). Following the scanning, participants rated the perceived pain intensity and unpleasantness to the stimulations of innocents and shared money with other innocents (Fig. 1F). We expected that participants would exhibit enhanced empathy and generosity towards innocents sharing preferences with fair (vs. unfair) targets, indicating that participants considered the broader social structure that encompassed the direct relations between themselves and the targets, as well as the indirect relations between these targets and the innocents. The influence of social structure on empathic and altruistic responses would be linked to changes in the activity of regions responsible for emotional regulation (e.g., dmPFC and IPFC), which enabled flexible vicarious emotional responses based on social relations. Furthermore, we hypothesized that social structure would alter neural patterns in response to the pain of different innocents in regions crucial for emotional processing (e.g., AI), in addition to the functional connectivity between these regions and those involved in emotional regulation, reflecting the top-down regulation of low-level affective processing by higher-order cognitive processes.

2. Methods and materials

2.1. Participants

Twenty-seven Chinese healthy college students (16 females) (mean age $\pm$ S.D. = 22.41 $\pm$ 1.78 years) from Beijing Normal University participated in this study and completed the fMRI scanning for monetary compensation. All participants were right-handed, had normal or corrected-to-normal visions, and had no history of neurological or psychiatric disorders. Written informed consent was obtained for all participants. The study was conducted in accordance with the 1964 Helsinki Declaration and its later amendments and was approved by the Ethics Committee of Beijing Normal University. The sample size was based on previous fMRI studies on the similar topic (Azevedo et al., 2013; Wu et al., 2024) and resource constraints. The power sensitivity analysis was conducted with MorePower software (Campbell and Thompson, 2012). Using a 2×2 repeated-measures analysis of variance (ANOVA), effect sizes in the moderate-to-large range ($\eta_p^2 \geq 0.246$, repeated measures (RM) = 2×2 , $\alpha = 0.05$, $1 - \beta = 0.80$) can be reliably detected given the current sample size (Bakeman, 2005).

2.2. Procedures

2.2.1. Social structure construction tasks

This study consisted of two sessions (Fig. 1). In the first session, participants were invited to complete a series of social structure building tasks one day prior to the fMRI scanning. Participants first completed a time estimation task (Feng et al., 2017; Miltner et al., 1997) to earn monetary units in collaboration with putative partners (Fig. 1B). In this task, participants were required to estimate the duration of 1 s, and then their performance on each trial would be randomly paired with that of a partner. Only when both of them responded within a certain critical time interval were they deemed correct and awarded a joint reward from experimenters, which would later be utilized in subsequent dictator game (DG) (Kahneman et al., 1986). This task required participants and

their partners to strive towards a common goal, thus creating an experimental scenario that facilitated the establishment of direct relationships (fair or unfair) in the DG. Covertly, the feedback of this task was adaptively adjusted to maintain an accuracy of 50% for each participant (Boksem et al., 2011), ensuring that equal contributions and rewards for all participants. Afterwards, participants proceeded to an aesthetic preference task (Tajfel et al., 1971), designed to establish similarity relationships with others. They were presented with twenty-seven pairs of images featuring the artistic styles of Klee, Mondrian, and Kandinsky (Fig. 1C). On each trial, participants were asked to select their preferred image from each pair, and they were told that their aesthetic preferences would be determined by their selections. Unbeknownst to participants, their aesthetic preferences were randomly assigned in the experiment.

In the second session (Fig. 1), each participant's aesthetic preference was first assigned to a particular artistic style, represented by colors: Klee (yellow), Mondrian (green), or Kandinsky (blue). Additionally, participants were informed that many individuals had previously participated in the aesthetic preference task and that they would subsequently interact with individuals who had different aesthetic preferences, specifically, those who favored the other two artistic styles. Notably, with respect to dyadic similarity, it was expected that participants would treat individuals who exhibited the other two aesthetic preferences similarly.

Afterwards, participants acted as passive recipients in the DG to establish direct relationships with the dictators (Kahneman et al., 1986) (Fig. 1D). In this task, they observed how dictators (target players) with the other two aesthetic preferences distributed the jointly earned money (10 yuan) from the time estimation task. Importantly, participants received fair allocations (i.e., self: other, 4:6 or 5:5) from dictators with one aesthetic preference while receiving unfair allocations (1:9 or 2:8) from dictators with another aesthetic preference.

2.2.2. Empathy for pain task

During the fMRI scanning session, participants took part in an empathy for pain task. In this task, participants were presented with four different 'innocents' (one male and one female per aesthetic preference, innocent players) who shared aesthetic preferences with either the fair or unfair dictators but had no prior interactions with the participants. In these photographs of innocents receiving painful and non-painful stimulation, participants were required to empathize and judge whether or not these presented innocents were experiencing pain (Fig. 1E). Notably, emotional facial expressions of innocents were held constant across the pain and no-pain conditions to ensure that participants focused on contextual cues—namely, whether the stimulation was painful (needle) or non-painful (Q-tip)—rather than on facial expressions. This design is consistent with established approaches in the empathy for pain literature (Lamm et al., 2011; Singer et al., 2006; Xu et al., 2009). While such tasks inherently rely on semantic knowledge about the painfulness of different stimuli, accumulating evidence indicates that they nonetheless effectively elicit emotional empathic responses. Specifically, neural responses evoked by these paradigms overlap with those engaged during first-hand pain experiences (Lamm et al., 2011), are shaped by affective and motivational evaluations of others (Singer et al., 2006), and correlate with individual differences in emotional awareness and sharing (Feng et al., 2016).

Participants were explicitly informed that these innocents did not participate in the DG, but their aesthetic preferences were indicated by different colored frames surrounding their photographs. To eliminate potential confounding factors, such as attractiveness, the associations between innocents and their aesthetic preferences were counter-balanced across participants. Each trial began with a central fixation (1 s) followed by a photograph with a colored frame. Participants were instructed to assess within 3 s whether the presented innocent was in pain (de Greck et al., 2012). Each trial ended with an inter-trial interval lasting between 1 and 3 s. This task was composed of two scanning runs,

each containing 64 trials: 8 trials for each innocent receiving painful and non-painful stimulation, totaling 16 trials per condition. All conditions were randomly presented on a trial-by-trial basis.

2.2.3. Post-scan rating

After the fMRI scanning, participants were presented with the photographs of innocents again and were asked to rate two questions using a 9-point Likert scale. The first question, perceived pain intensity (“how painful do you think the individual feels”, 1 = not at all, 9 = extremely painful), targeted cognitive-evaluative aspects associated with pain. The second question, unpleasantness (“how unpleasant do you feel when observing the photograph”, 1 = extremely pleasant, 9 = extremely unpleasant), targeted aspects of empathy related to affective sharing and vicarious distress. These questions also align with the constructs of emotion identification and affective sharing in the proposed empathy model of Coll (Coll et al., 2017).

2.2.4. Post-scan DG task

In the final phase, participants took on the role of a dictator in the DG, distributing the jointly earned rewards (10 yuan) to other new passive innocent recipients who held the other two aesthetic preferences. It's essential to note that participants were clearly informed that these innocent recipients were not the dictators in the pre-scan DG or the innocents in the empathy for pain task (Fig. 1F).

In summary, participants had direct interactions only with fair and unfair targets during the pre-scan DG. In contrast, the innocents encountered during the fMRI session and post-scan DG were entirely novel, with no prior interactions with the participants. Participants were clearly aware of the distinction between these innocents and the previously encountered targets. Moreover, all innocents differed from participants in aesthetic preferences, eliminating any direct self-other similarity that could have influenced empathic or altruistic responses. Thus, if participants had relied solely on self-other relations, their responses toward innocents would be unbiased.

2.3. Stimuli

For the pre-scan DG task, we selected 16 distinct neutral faces (8 male) from the Chinese Facial Affective Picture System (CFAPS; Gong et al., 2011). These images, uniformly sized at 159×198 pixels, served as the targets with whom participants established direct, dyadic relationships during the task. In the empathy for pain task, participants viewed 64 photographs depicting four “innocent” individuals (2 male) who had no prior interactions with the participants. For each innocent, 16 images were presented, including 8 depicting painful stimulation (needle penetration to the left or right cheek; 4 images per side) and 8 depicting non-painful stimulation (Q-tip touch to the left or right cheek; 4 images per side). These images, standardized to 298×298 pixels, were adapted from validated video clips originally developed by Xu et al. (2009), which have been shown to reliably elicit empathic neural and behavioral responses. For the post-scan DG task, an additional set of 16 neutral faces (8 male) was selected from the CFAPS. These faces, sized at 159×198 pixels, were distinct from those used in the pre-scan DG and served as novel, unencountered innocents.

2.4. Data acquisition

Imaging data were acquired with a 3T Siemens Trio scanner equipped with a 12-channel head coil at Imaging Center for Brain Research in Beijing Normal University. A T2-weighted gradient-echo-planar-imaging sequence was used to acquire functional images (TR/TE = 2000 ms/30 ms, flip angle = 90° , number of axial slices = 33, slice thickness = 3.5 mm, gap between slices = 0.7 mm, matrix size = 64×64 , FOV = 224×224 mm²). High-resolution anatomical images covering the entire brain were also obtained by a magnetization prepared rapid acquisition with gradient-echo sequence (TR/TE = 2530/3.39 ms, flip angle = 7° ,

number of sagittal slices = 144, slice thickness = 1.33 mm, matrix size = 256×256 , FOV = 256×256 mm²).

2.5. Behavioral data analysis

Behavioral data analyses were carried out using SPSS 26.0 with a significance threshold of $p < 0.05$ (two-tailed). Participants' performance in empathy for task, including accuracy rate and response time, as well as subjective ratings of pain intensity and unpleasantness in post-scan rating task, were submitted to a 2 (Innocents: innocents resembling fair targets (IF) vs. innocents resembling unfair targets (IU)) $\times$ 2 (Stimulation: painful stimulation (Pain) vs. non-painful stimulation (No-Pain)) repeated measures analysis of variance (ANOVA). Finally, a paired *t*-test was conducted to examine the differences in altruistic giving to innocents resembling fair or unfair targets in the post-scan DG.

2.6. fMRI data analysis

Functional neuroimaging data analyses were performed with SPM12 (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>). Preprocessing of functional data included realignment through rigid-body registration to correct for head motion, spatial normalization to the Montreal Neurological Institute template with a resolution of $2 \times 2 \times 2$ mm³, spatial smoothing (FWHM = 8 mm) and temporal high-pass filtering (removal of low frequency drift of $T > 128$ s).

A two-level general linear model (GLM) was used to analyze functional data. The first-level modeling included regressors defined for each participant. These regressors modeled blood oxygenation level-dependent responses to five different types of events: painful stimulation applied to the innocents resembling fair targets (IF-P), non-painful stimulation applied to the innocents resembling fair targets (IF-NP), painful stimulation applied to the innocents resembling unfair targets (IU-P), non-painful stimulation applied to the innocents resembling unfair targets (IU-NP), and non-responded trials. Additional covariates of no interest included frame-wise displacement and intensity outliers using the *Artifact Detection Toolbox* (https://www.nitrc.org/projects/artifact_detect). Each trial was time-locked to the onset of the photographs with a duration of 3 s and modeled using a canonical hemodynamic response function (HRF) (Büchel et al., 1998). To improve noise estimation, the GLM also considered signal temporal autocorrelations with a first-order autoregressive model (Bullmore et al., 1996). And then First-level contrasts of the parameter estimates were calculated for the main effects of Stimulation (Pain vs. No-pain), Innocents (IF vs. IU), and their Interaction (IF-P vs. IU-P – IF-NP vs. IU-NP). These contrasts were then entered into a random-effects second-level analysis using a one-sample *t*-test to enable population-level inferences.

2.6.1. Univariate activation analysis

Whole-brain statistical parametric mapping analyses were conducted to identify brain areas modulated by main effects of Innocents, Stimulation and their interaction. Parameter estimates of identified regions were extracted using the *REX toolbox* (<https://www.nitrc.org/projects/rex>). To control for false positive control, the statistical threshold was set at a threshold of $p < 0.001$ at the voxel level and FWE corrected threshold of $p < 0.05$ at the cluster level (Eklund et al., 2016; Woo et al., 2014).

2.6.2. Multi-voxel pattern analysis

To explore brain regions where neural patterns differentiated between painful stimulation of innocents resembling fair or unfair targets, we performed the Multi-voxel pattern analysis (MVPA) using *The Decoding Toolbox* (Hebart et al., 2014). Compared to conventional univariate analysis, MVPA is more sensitive to information carried in distributed response patterns and uncovers the information content of brain regions. Searchlight analysis was used to identify local distribution patterns (Jolly and Chang, 2021). For each participant, we estimated a

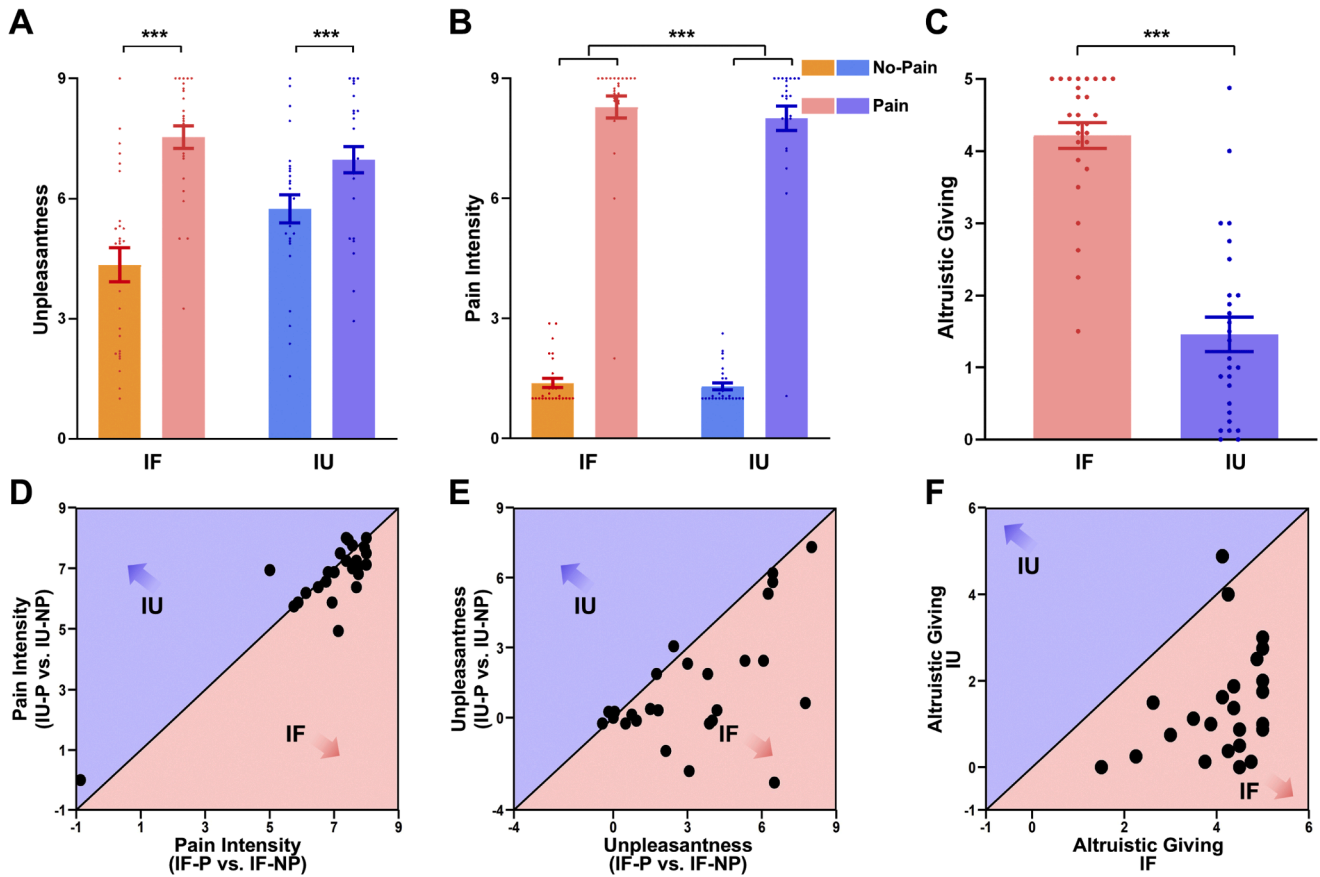


Fig. 2. The behavioral results. A Self-reported ratings of perceived pain intensity as a function of Innocents and Stimulation. Participants reported higher ratings of pain intensity for painful than for non-painful stimulation. B Self-reported ratings of unpleasantness as a function of Innocents and Stimulation. Participants reported higher ratings of unpleasantness to the pain (vs. no-pain) of innocents resembling fair targets than that of innocents resembling unfair targets. C Average amounts of altruistic giving in the post-scan Dictator Game as a function of the Innocents. Participants allocated higher amounts of money to innocents resembling fair targets. D Scatter plot of differences in pain intensity ratings (pain vs. no-pain) between innocents resembling fair and unfair targets. Each point corresponds to mean difference score of a single participant for innocents resembling fair (x axis) and unfair targets (y axis). Points on the diagonal represent participants whose difference score was equal between two types of innocents. Points below the diagonal colored in pink represent participants for whom difference score was higher for innocents resembling fair targets. Points above the diagonal colored in purple represent participants for whom difference score was higher for innocents resembling unfair targets. E Scatter plot of differences in unpleasantness ratings (pain vs. no-pain) between innocents resembling fair and unfair targets. F Scatter plot of altruistic giving between innocents resembling fair targets and unfair targets. *** $p < 0.0005$. Error bars indicate standard error. IF, innocents resembling fair targets; IU, innocents resembling unfair targets; IF-P, painful stimulation to innocents resembling fair targets; IU-P, painful stimulation to innocents resembling unfair targets; IF-NP, non-painful stimulation to innocents resembling fair targets; IU-NP, non-painful stimulation to innocents resembling unfair targets.

GLM in which trials of four conditions were individually modeled with the exception that non-response trials were combined into an additional condition. The estimated beta maps were fed to a support vector machine (SVM) classifier with a fixed cost parameter ($c = 1$) and searchlight decoding scheme (Corradi-Dell'Acqua et al., 2011; Kriegeskorte et al., 2006). For each voxel in the individual participants' brain image in the native space, a sphere with a radius of four voxels was defined. For painful and non-painful stimulation separately, the parameter estimates associated with the two types of innocents (IF or IU) for each of the N voxels in a given sphere were then extracted to represent an N -dimensional pattern vector. Pattern vectors in one run (training set) were employed to train the SVM to discriminate the innocents resembling fair or unfair targets, and the performance of the classifier was measured on the other independent run (test set). The accuracy was computed as a metric of the sensitivity of the classifier to discriminate experimental conditions in the test set (Corradi-Dell'Acqua et al., 2011; Corradi-Dell'Acqua et al., 2016). The procedure was repeated twice, with each run being the test set once. The mean accuracy across two folds was calculated and assigned to the central voxel of the sphere. The classification was conducted for each voxel, resulting in a 3-D accuracy map for each participant. At the group level, the classification performance of

the innocents resembling fair or unfair targets in the painful condition was compared to that of innocents resembling fair or unfair targets in the non-painful condition using a paired-t-test. The statistical significance was determined using a permutation test ($N = 5000$) implemented with the *SnPM* toolbox of *SPM* (Corradi-Dell'Acqua et al., 2011; Corradi-Dell'Acqua et al., 2016).

Moreover, we conducted a complementary whole-brain MVPA to identify global brain patterns decoding painful or non-painful stimulation of the two types of innocents (Kohoutová et al., 2020; Zhou et al., 2020). In particular, we used linear SVM to train whole-brain multi-variate pattern classifiers to distinguish between innocents resembling fair or unfair targets separately for painful and non-painful conditions (that is, IF-P vs. IU-P and IF-NP vs. IU-NP), using the *Canlab* toolbox (<https://github.com/canlab/CanlabCore>). The classifiers were trained on each participant's first-level contrast images for two different conditions, where IF-P and IU-P were respectively decoded as 1 and -1 in one classification model, while IF-NP and IU-NP were respectively decoded as 1 and -1 in another classification model. To evaluate the performance of the algorithm, a leave-one-subject-out cross-validation procedure was used to divide the sample into a training set (all but one participant) and a test set (the test participant). The classification

accuracy of the SVM classifiers was assessed using the two-choice test, where the pattern expression values (that is, the dot-product of a vectorized activation image with the classifier weights) were compared for two conditions tested within the same out-of-sample individual and then the higher value was chosen as IF-P in IF-P vs. IU-P or IF-NP in IF-NP vs. IU-NP (Zhou et al., 2021). The areas under the receiver operating characteristic curves were employed to visualize the performance of classifiers.

Both MVPA and univariate analyses utilize mean activation, but MVPA also captures voxel-level variability, even if a single voxel does not significantly change across conditions. In this study, we report both univariate and MVPA analyses for two main reasons. First, univariate analysis is the conventional standard in the literature, allowing for direct comparison with previous findings and supporting future meta-analyses. Second, MVPA and univariate approaches are sensitive to different variances, noise sources and different types of effects (Davis et al., 2014)

2.6.3. Connectivity analysis

Focusing on the regions identified in the univariate activation and MVPA with local patterns, an analysis of psychophysiological interaction (PPI) (Friston et al., 1997) was implemented to examine how social structure modulates the functional coupling between the identified regions and other areas. Specifically, regions-of-interest (ROIs) were defined as a sphere with a 4 mm radius centered at the center voxel of the revealed regions. The fMRI signal time courses were then individually extracted from these ROIs as the seeding signals with the *generalized PPI* toolbox (<http://www.nitrc.org/projects/gppi>, version 13.1) (McLaren et al., 2012). These seeding signals were further deconvolved with the canonical HRF, resulting in estimates of underlying neuronal activity (Gitelman et al., 2003). Subsequently, the interactions of these estimated neuronal time-series and vectors representing each of the onsets for each regressor and corresponding parametric modulators were computed. Lastly, these interaction terms were re-convolved with the HRF and entered into a new GLM along with the vectors for the onsets of each event (i.e., the psychological terms). Group level analysis of the PPI data was similar to that of the activation data, except that the beta values used were derived from the PPI regressors. In this analysis, we focused on the interaction of Innocents and Stimulation.

2.6.4. Correlation

Finally, to examine potential brain-behavior associations, Pearson correlation coefficient (r) was computed to determine correlations among behavioral (self-reported ratings, altruistic giving) and neuro-imaging (activation, decoding accuracy, connectivity strengths) measures. Given the exploratory nature of these analyses, no multiple comparisons correction was applied.

3. Results

3.1. Modulations of social structure on empathic and altruistic behaviors

In the empathy for pain task during fMRI scanning, the accuracy of identification of painful and non-painful stimuli was high and did not differ between innocents (innocents resembling fair targets (IF): $98.1\% \pm 1.2\%$; innocents resembling unfair targets (IU): $97.7\% \pm 1.2\%$; $F(1, 26) = 0.41$, $p = 0.52$, $\eta_p^2 = 0.02$) or types of stimulation (Pain (P): $97.9\% \pm 1.1\%$; No-Pain (NP): $97.8\% \pm 1.1\%$; $F(1, 26) = 0.51$, $p = 0.82$, $\eta_p^2 = 0.002$). The interaction between them was not significant either ($F(1, 26) = 3.26$, $p = 0.08$, $\eta_p^2 = 0.11$, Fig. S1A). The response time to painful stimuli was longer than that to non-painful stimuli (Pain: $1.50 \text{ s} \pm 0.08$; No-Pain: $1.34 \text{ s} \pm 0.06$; $F(1, 26) = 10.70$, $p = 0.003$, $\eta_p^2 = 0.29$). The main effect of Innocents (IF: $1.43 \text{ s} \pm 0.07$; IU: $1.42 \text{ s} \pm 0.07$; $F(1, 26) = 0.22$, $p = 0.65$, $\eta_p^2 = 0.008$) or the interaction ($F(1, 26) = 3.06$, $p = 0.092$, $\eta_p^2 = 0.11$, Fig. S1B) was not significant.

In the post-scan rating task, the ratings of pain intensity were higher for painful than non-painful stimulation (Pain: 8.15 ± 0.28 ; No-Pain:

Table 1

Brain regions that were identified using various analysis methods.

Brain Regions	MNI Coordinates of Local Maxima (mm)			Local Maxima	Cluster Size (voxel)
	x	y	z		
Univariate activation analysis					
Main effect of Stimulation					
Pain > No-Pain					
R precentral gyrus extending to insula	50	8	46	7.87	3279
R middle occipital gyrus	28	-96	-2	7.84	2782
L/R supplementary motor area	4	18	66	5.87	1494
L/R dorsomedial prefrontal cortex	4	56	34	6.80	308
L middle occipital gyrus	-18	-102	-6	7.36	2513
L insula	-22	-2	4	5.45	2197
L hippocampus	-32	-16	-10	5.38	264
L precentral gyrus	-30	0	44	4.80	465
L dorsal anterior cingulate	-14	24	22	4.76	191
Interaction effect					
(IU-P - IF-P) > (IU-NP - IF-NP)					
R dorsomedial prefrontal cortex	12	48	26	4.64	257
R temporoparietal junction	40	-56	32	4.64	206
L ventromedial prefrontal cortex	-18	54	-8	4.91	257
L lateral prefrontal cortex	34	24	32	4.58	357
MVPA searchlight analysis					
(IU-P vs. IF-P) - (IU-NP vs. IF-NP)					
L anterior insula	-38	18	-6	5.12	1088
L premotor cortex	-28	0	38	4.85	872
IU-P vs. IF-P					
L anterior insula	-46	24	-10	4.82	764
L premotor cortex	-32	6	56	5.43	949
L middle occipital gyrus	-26	-92	0	5.26	2050
Connectivity analysis					
Interaction effect					
(IF-P - IU-P) > (IF-NP - IU-NP)					
Lateral prefrontal cortex as the seed region					
primary somatosensory cortex /primary motor	-44	-24	54	5.02	252
Anterior insula as the seed region					
subgenual anterior cingulate cortex	6	20	-4	5.29	164
Premotor cortex as the seed region					
lateral prefrontal cortex	34	50	8	4.58	146

$p < 0.05$ whole-brain FWE-corrected at the cluster level.

1.35 ± 0.09 , $F(1, 26) = 485.84$, $p = 2.38 \times 10^{-18}$, $\eta_p^2 = 0.95$, Fig. 2A & 2D). The main effect of Innocents (IF: 4.84 ± 0.13 ; IU: 4.66 ± 0.17 ; $F(1, 26) = 2.81$, $p = 0.11$, $\eta_p^2 = 0.10$) or the interaction ($F(1, 26) = 1.79$, $p = 0.20$, $\eta_p^2 = 0.06$) was not significant. Ratings of unpleasantness were higher for painful than non-painful stimulation (Pain: 7.25 ± 0.25 ; No-Pain: 5.04 ± 0.36 , $F(1, 26) = 25.81$, $p = 2.7 \times 10^{-5}$, $\eta_p^2 = 0.50$, Fig. 2B & 2E), while there was no difference in unpleasantness between innocents (IF: 5.94 ± 0.26 ; IU: 6.36 ± 0.24 ; $F(1, 26) = 3.88$, $p = 0.059$, $\eta_p^2 = 0.13$). The interaction effect was significant ($F(1, 26) = 16.75$, $p = 3.67 \times 10^{-4}$, $\eta_p^2 = 0.39$), such that participants reported a higher level of unpleasantness to painful (vs. non-painful) stimulation of innocents resembling fair targets than that of innocents resembling unfair targets.

In the post-scan DG task, participants exhibited greater generosity toward innocents resembling fair targets by offering them a greater amount of money, although they had never directly interacted with

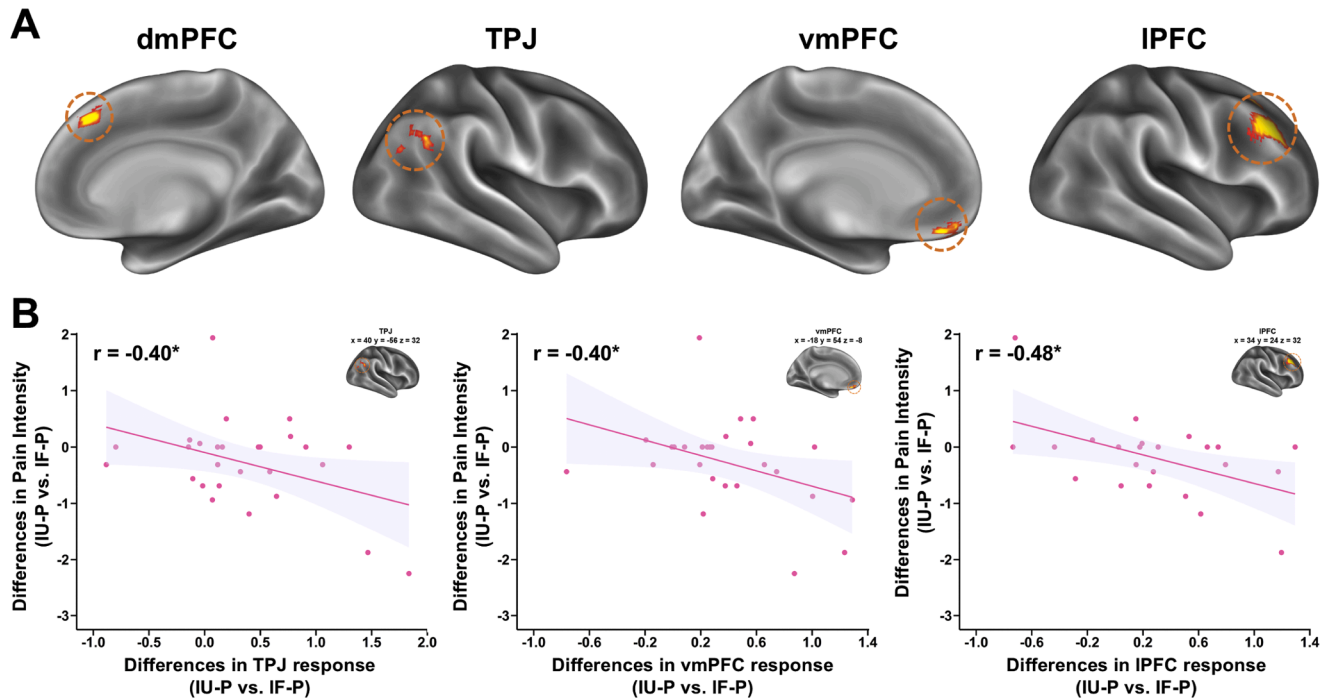


Fig. 3. fMRI results of univariate activation analysis. **A** Activation revealed by the interaction (IU-P vs. IF-P) - (IU-NP vs. IF-NP). A voxel-level threshold of $p_{\text{uncorrected}} < 0.001$ and a cluster-level threshold of $p_{\text{FWE}} < 0.05$. **B** The correlation between the activation of the TPJ, vmPFC, and IPFC and perceived pain intensity regarding the difference between the pain of innocents resembling unfair and fair targets. $^*p < 0.05$. The red line in each scatter plot represents the fitted line; the upper and lower bounds indicate a 95% confidence interval. dmPFC, dorsomedial prefrontal cortex; TPJ, temporoparietal junction; vmPFC, ventromedial prefrontal cortex; IPFC, lateral prefrontal cortex; IF-P, painful stimulation to innocents resembling fair targets; IU-P, painful stimulation to innocents resembling unfair targets; IF-NP, non-painful stimulation to innocents resembling fair targets; IU-NP, non-painful stimulation to innocents resembling unfair targets.

those innocents before (IF: 4.22 ± 0.93 ; IU: 1.46 ± 1.26 ; $t(26) = 11.07$, $p = 2.48 \times 10^{-11}$, Cohen's $d = 2.13$, Fig. 2C & F).

In short, participants' empathic responses (i.e., pain versus no-pain) and altruistic giving were modulated by whether innocents—who had no prior interactions with the participants—shared aesthetic preferences with previously encountered fair or unfair targets. Crucially, these effects cannot be explained solely by direct self-other relationships, as all innocents differed from participants in their own aesthetic preferences. Instead, the findings reflect participants' sensitivity to social structure, which is represented through the integration of their own direct experience with the targets (i.e., fair vs. unfair treatment) and the indirect relationship between innocents and those targets (i.e., shared preferences between innocents and fair/unfair targets).

3.2. Social structure alters univariate brain responses to empathic pain in the mPFC, IPFC, and TPJ

For the main effect of Stimulation (Pain > No-Pain, Table 1 and Fig. S2), significant activations were identified in the bilateral insula, dmPFC, supplementary motor area, middle occipital gyrus, precentral gyrus, left dorsal ACC, and hippocampus. These results align with previous meta-analytic findings on the brain systems supporting empathy for pain (Fallon et al., 2020; Jauniaux et al., 2019; Lamm et al., 2011), further validating the effectiveness of the pain judgment task in eliciting empathic responses. The reverse contrast of No-Pain > Pain revealed no significant activation. Moreover, the main effect of Innocents (IF > IU or IU > IF) yielded no significant activation.

The interaction between Innocents and Stimulation defined by the contrast of [(IU-P vs. IF-P) - (IU-NP vs. IF-NP)] revealed significant activation in the dmPFC, TPJ, ventromedial PFC (vmPFC), and IPFC (Fig. 3A), with a cluster-defining threshold of $p < 0.001$ and a Family Wise Error (FWE) corrected threshold of $p < 0.05$ at the cluster level. That is, these regions showed stronger responses to the pain (vs. no-

pain) of innocents resembling unfair targets than that of innocents resembling fair targets. In addition, the differences in the activations of the TPJ ($r = -0.40$, $p = 0.038$), vmPFC ($r = -0.40$, $p = 0.041$), and IPFC ($r = -0.48$, $p = 0.012$) between the pain of innocents resembling unfair (vs. fair) targets were negatively correlated with differences in perceived pain intensity between the pain of innocents resembling unfair (vs. fair) targets (Fig. 3B). In other words, the higher activity of these regions to painful stimulation of innocents resembling unfair (vs. fair) targets, the lower perceived pain intensity to painful stimulation of innocents resembling unfair (vs. fair) targets.

3.3. Social structure modulates multivariate brain responses to empathic pain in the AI and PMC

For the local patterns, the results revealed that neural patterns in the AI and the premotor cortex (PMC) showed more robust and distinct discriminations between painful stimulation of the two types of innocents compared to non-painful stimulation of the two types of innocents ($p < 0.05$ whole-brain corrected at the cluster level, Fig. 4A & 4B and Table 1).

These regions were selectively involved in discriminating two types of innocents in the painful stimulation but not in the non-painful stimulation. Specifically, brain regions where local activation patterns significantly discriminated the pain of two types of innocents revealed the AI, the PMC, and middle occipital gyrus ($p < 0.05$ whole-brain corrected at the cluster level, Fig. 4C and Table 1). However, the classification model discriminating the non-painful stimulation of two types of innocents revealed no significant regions.

The classifier based on whole-brain patterns aligned with our MVPA findings with local patterns. In particular, the classifier demonstrated an 85% accuracy (95% confidence interval (CI): 78.4% - 91.8%), 85% sensitivity (95% CI: 69%–97%), 85% specificity (95% CI: 71%–96%) in discriminating painful stimulation of the two types of innocents (area

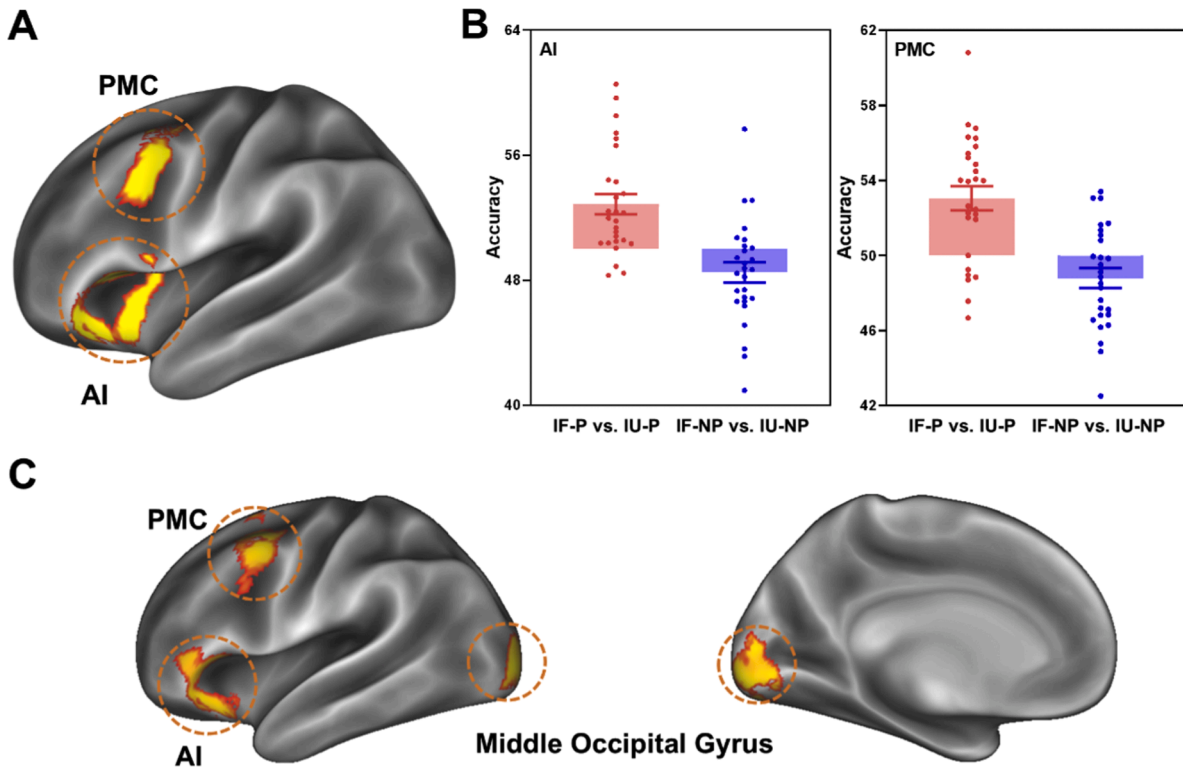


Fig. 4. fMRI results of MVPA with local neural patterns. **A** Neural patterns in the AI and PMC exhibiting higher discriminations of two types of innocents in the painful condition than in the non-painful condition. **B** The accuracy of the AI (left) and PMC (right) in discriminating innocents resembling fair or unfair targets under painful and non-painful conditions. **C** Neural patterns in the AI, PMC, and middle occipital gyrus enabled classification between the pain (but not no-pain) of the two types of innocents. A voxel-level threshold of $p_{\text{uncorrect}} < 0.001$ and a cluster-level threshold of $p_{\text{FWE}} < 0.05$. Error bars indicate standard error. AI, anterior insula; PMC, premotor cortex; IF-P, painful stimulation to innocents resembling fair targets; IU-P, painful stimulation to innocents resembling unfair targets; IF-NP, non-painful stimulation to innocents resembling fair targets; IU-NP, non-painful stimulation to innocents resembling unfair targets.

under curve (AUC) = 0.90, $p = 3.11 \times 10^{-4}$, Fig. 5A & C). Moreover, the classification scores were positively correlated with differences in perceived pain intensity scores between two types of innocents ($r = 0.44$, $p = 0.002$, Fig. 5B). That is, stronger whole-brain neural discriminations were associated with larger differences in perceived pain intensity.

However, the classifier performed at chance level in discriminating non-painful stimulation of the two types of innocents (accuracy = 63%, with 95% CI: 53.7% – 72.3%, sensitivity = 63%, with 95% CI: 44% – 81%, specificity = 63%, with 95% CI: 45% – 81%, AUC = 0.75, $p = 0.25$, Fig. 5A & D).

3.4. Social structure regulates the functional connectivity in empathic pain processing

For the IPFC identified in the univariate activation analysis, the contrast of [(IF-P vs. IU-P) > (IF-NP vs. IU-NP)] identified primary somatosensory cortex /primary motor cortex (S1/M1, $p < 0.05$ whole-brain corrected at the cluster level, Fig. 6A and Table 1). That is, functional connectivity between the IPFC and the S1/M1 was stronger to the pain (vs. no-pain) of innocents resembling fair targets than that of innocents to unfair targets. The differences in IPFC-S1/M1 connectivity between the pain of two types of innocents were positively correlated with differences in altruistic giving ($r = 0.39$, $p = 0.047$, Fig. 6D). That is, the greater the connectivity between IPFC and S1/M1 in response to the pain of innocents resembling fair (compared to unfair) targets, the more money participants shared with innocents resembling fair (compared to unfair) targets.

For the AI identified in the searchlight MVPA, the contrast of [(IF-P vs. IU-P) > (IF-NP vs. IU-NP)] identified subgenual anterior cingulate cortex (sgACC, $p < 0.05$ whole-brain corrected at the cluster level,

Fig. 6B & 6E and Table 1). The stronger AI-sgACC connectivity was associated with higher perceived pain intensity to the pain of the innocents resembling fair (vs. unfair) targets ($r = 0.39$, $p = 0.046$, Fig. 6E).

For the PMC identified in the searchlight MVPA, the contrast of [(IF-P vs. IU-P) > (IF-NP vs. IU-NP)] identified IPFC ($p < 0.05$ whole-brain corrected at the cluster level, Fig. 6C and Table 1). The correlational analysis revealed no significant association between the strength of PMC-IPFC connectivity and changes in altruistic behavior ($p > 0.05$).

4. Discussion

The current study examined the neural substrates underlying the impact of social structure on the empathy for pain and altruistic behaviors. At the behavioral level, participants reported a higher unpleasantness to painful (vs. non-painful) stimulation of innocents resembling fair targets than that of innocents resembling unfair targets. Likewise, participants were more generous toward innocents resembling fair targets by offering them a greater amount of money. At the neural level, compared to painful (vs. non-painful) stimulation of innocents resembling fair targets, painful stimulation of innocents resembling unfair targets elicited heightened activation in regions crucial for emotion regulation, including the dmPFC, TPJ, IPFC, and vmPFC. The higher activity of these regions to painful stimulation of innocents resembling unfair (vs. fair) targets, the lower perceived pain intensity to painful stimulation of innocents resembling unfair (vs. fair) targets. Furthermore, local multi-voxel patterns in regions associated with emotion processing and sensorimotor processing (AI, PMC) discriminated painful stimulation but not non-painful stimulation of the two types of innocents. Similarly, whole-brain neural patterns distinguished painful stimulation but not non-painful stimulation of the two types of innocents, with stronger whole-brain neural discriminations linking to

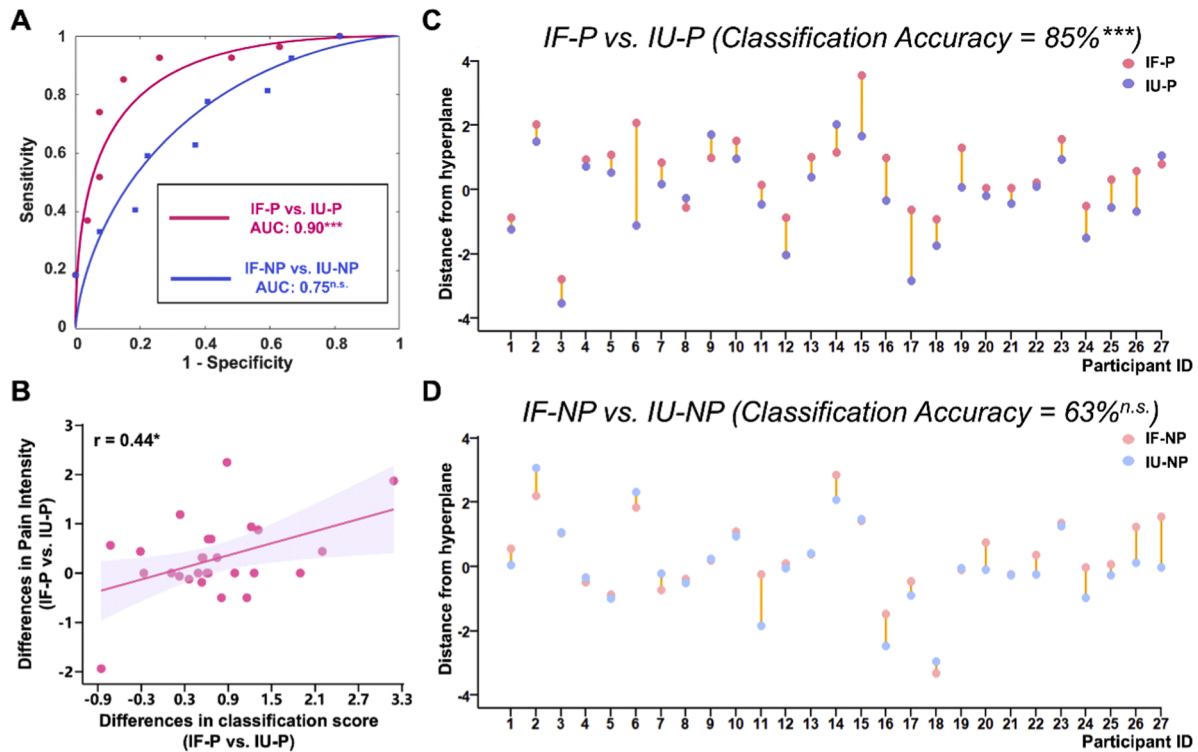


Fig. 5. fMRI results of MVPA with whole-brain neural patterns. **A** Receiver operating characteristic curves (ROC) of IF-P vs. IU-P classifier and IF-NP vs. IU-NP classifier. **B** The correlation between the classification score and perceived pain intensity regarding the difference between the pain of innocents resembling fair and unfair targets. The red line represents the fitted line; the upper and lower bounds indicate a 95% confidence interval. **C** Cross-validated (leave-one-subject-out) distance from IF-P and IU-P to hyperplane for each participant. **D** Cross-validated (leave-one-subject-out) distance from IF-NP and IU-NP to hyperplane for each participant. * $p < 0.05$; *** $p < 0.0005$; n.s., not significant; AUC, area under curve; IF-P, painful stimulation to innocents resembling fair targets; IU-P, painful stimulation to innocents resembling unfair targets; IF-NP, non-painful stimulation to innocents resembling fair targets; IU-NP, non-painful stimulation to innocents resembling unfair targets.

larger differences in self-reported pain intensity. Lastly, the functional coupling between IPFC and sensorimotor areas (PMC, M1/S1) as well as between AI and sgACC were enhanced in response to the pain (vs. no-pain) of innocents resembling fair (vs. unfair) target. The stronger functional connectivity between these regions to painful stimulation of innocents resembling fair (vs. unfair) targets, the higher perceived pain intensity to painful stimulation of innocents resembling fair (vs. unfair) targets, and the larger amounts of money shared with innocents resembling fair (vs. unfair) targets. Taken together, the current findings provide the first evidence to uncover neural substrates through which human empathic responses and altruistic giving are modulated by social structure beyond the self-other direct relationships.

Our findings indicate that the influence of social structure on empathic and altruistic responses is mediated by the engagement of regions implicated in both emotion regulation and mentalizing. Notably, the dmPFC and TPJ are central to mentalizing processes, such as distinguishing self from others' experiences (Lamm et al., 2016, 2010; Parkinson et al., 2014), adopting others' perspectives (Meyer et al., 2012; Schnell et al., 2011), and tracking social distance or dissimilarity (Lawrence et al., 2006; Majdandžić et al., 2016; Mitchell et al., 2006). The increased activation of these regions when observing the suffering of innocents resembling unfair targets may reflect a social distancing mechanism—implemented through mentalizing—to justify reduced empathy. This interpretation is consistent with prior evidence that the dmPFC supports the down-regulation of empathic responses via intentional social distancing (Leiberg et al., 2012), and with our finding that TPJ activity negatively correlates with perceived pain intensity. In other words, regulatory processes in the dmPFC and TPJ may be enacted through mentalizing-based reinterpretations of others' mental states, traits, or group affiliations.

Additionally, the IPFC is involved in actively maintaining contextual goals by implementing top-down attention selection. Attentional processes involving the IPFC enable flexible emotional assessment by amplifying goal-relevant information and filtering out unwanted stimulus representations (Greening et al., 2014; Harris et al., 2013; Koban et al., 2017). The IPFC is particularly engaged when it is necessary to suppress the most salient stimulus attributes for flexible, context-dependent affective appraisal (Rudolf and Hare, 2014). Thus, the heightened IPFC activity could indicate a greater cognitive demand linked to redirecting attention away from the salient pain experienced by innocents resembling unfair targets. Conversely, when reacting to the pain of innocents resembling fair targets, participants might focus on the salient affective or sensorimotor information, which reduced the demand of cognitive control. In addition to the negative correlation between IPFC activity and perceived pain intensity for innocents resembling unfair targets, functional connectivity findings support this view as well, showing stronger functional connectivity between the IPFC and sensorimotor areas when responding to the pain of innocents resembling fair targets. That is, the IPFC seems to play a role in diverting attention from painful stimulation in innocents resembling unfair targets and, conversely, in concentrating attention on painful stimulation in innocents resembling fair targets.

Furthermore, the vmPFC is thought to function as a hub that synthesizes information across multiple brain systems to construct affective meaning, including brain networks involved in affective and peripheral processing as well as those involved in higher-level functions (Chang et al., 2021; Koban et al., 2017; Roy et al., 2012). Accordingly, the vmPFC is not important for reflexive emotional responses, but is essential when emotional responses are influenced by conceptual information regarding contextual demands, such as in cognitive

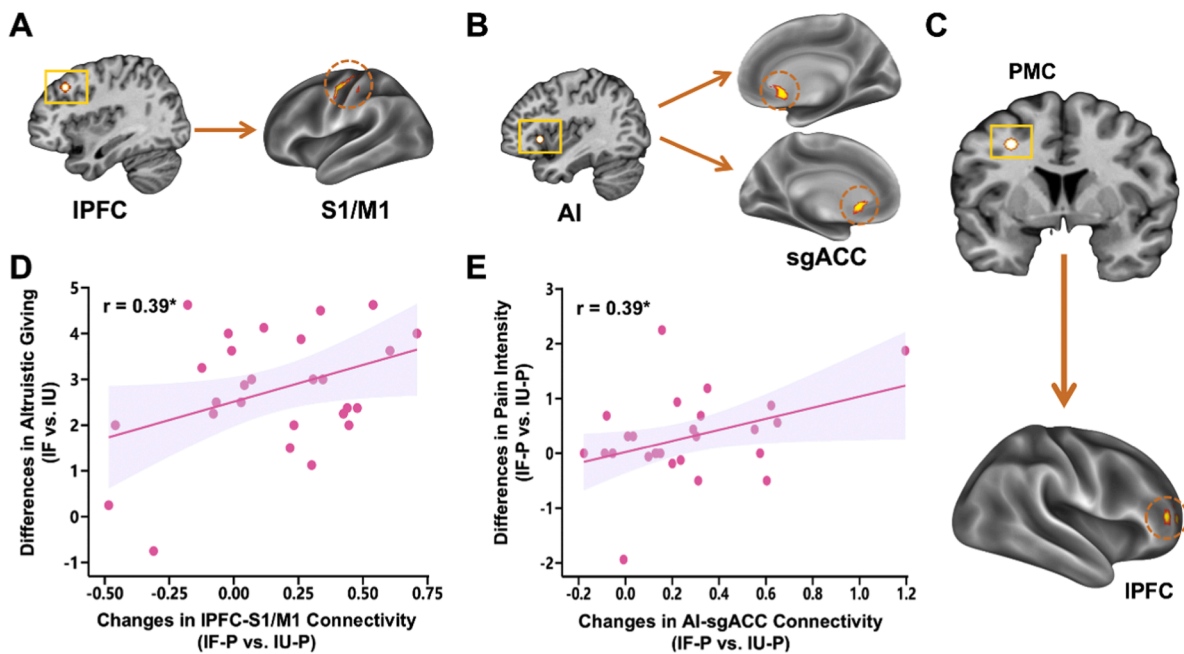


Fig. 6. The results of connectivity analysis. A Illustration of the seed region IPFC showing significant changes in functional coupling with the S1/M1 as revealed by the interaction of Innocents and Stimulation. B Illustration of the AI showing significant changes in functional coupling with the sgACC as revealed by the interaction of Innocents and Stimulation. C Illustration of the PMC showing significant changes in functional coupling with the IPFC as revealed by the interaction of Innocents and Stimulation. D The correlation between the strength of IPFC-S1/M1 connectivity and differences in altruistic giving between innocents resembling fair and unfair targets. A voxel-level threshold of $p_{\text{uncorrect}} < 0.001$ and a cluster-level threshold of $p_{\text{FWE}} < 0.05$. E The correlation between the strength of AI-sgACC connectivity and pain intensity regarding the difference between the pain of innocents resembling fair and unfair targets. $*p < 0.05$. The red line in each scatter plot represents the fitted line; the upper and lower bounds indicate a 95% confidence interval. IPFC, lateral prefrontal cortex; S1, primary somatosensory cortex; M1, primary motor cortex; AI, anterior insula; sgACC, subgenual anterior cingulate cortex; PMC, premotor cortex; IF, innocents resembling fair targets; IU, innocents resembling unfair targets; IF-P, painful stimulation to innocents resembling fair targets; IU-P, painful stimulation to innocents resembling unfair targets.

reappraisal tasks (Woo et al., 2015). Therefore, the heightened activity in the vmPFC might reflect a greater demand for reappraising vicarious emotional responses to the pain of innocents resembling unfair targets. The vmPFC might integrate social structure information encoded in the dmPFC and TPJ with contextual goals stored in the IPFC to generate contextually appropriate empathic responses.

In short, the engagement of the dmPFC, TPJ, IPFC, and vmPFC may reflect the implementation of multiple emotional regulation strategies, encompassing social distancing via mentalizing, attentional filtering, and affective reappraisal. These higher-level functions might in turn exert top-down regulation on affective and sensorimotor responses, enabling flexible vicarious emotional reactions to different innocents (Engen and Singer, 2013; Weisz and Zaki, 2018).

Our results support this hypothesis by first showing distinct neural patterns in brain regions associated with emotional and sensorimotor processing (AI and PMC) between painful stimulation of two types of innocents. The involvement of AI in perceiving others' pain is thought to reflect emotional sharing with others and constitutes the affective aspects of empathy (Bernhardt and Singer, 2012; Craig, 2009; Tu et al., 2023). The PMC is associated with motor imagery and action simulation (Braadbaart et al., 2014; Jolly and Chang, 2021), playing a key role in simulating and feeling painful states of others (Bernhardt and Singer, 2012). Importantly, the emotional and sensorimotor processes implemented in these regions are commonly engaged by somatic and vicarious pain (Lamm et al., 2011). Therefore, the discriminative neural patterns in the AI and PMC between the pain of two types of innocents suggest that participants were more readily to refer to their own pain feelings for sharing the pain of innocents resembling fair targets. In line with current findings, a large body of evidence has indicated the impact of self-other direct relations on the affective/sensorimotor aspects of empathy (Han, 2018), such that painful stimulation induced greater activity in the AI and sensorimotor regions for in-group members,

compared with out-group members (Akitsuki and Decety, 2009; Hein et al., 2010; Lamm et al., 2007). However, our study offers novel insights by not only demonstrating that the influence of social relations on empathy extends beyond direct relationships to encompass broader social structures but also revealing that the modified low-level representations of empathy for pain might arise from top-down cognitive control.

Our findings next demonstrated the modulations of social structure on the functional connectivity between regions involved in emotion regulation and those implicated in affective/sensorimotor processing. First, we observed enhanced functional connectivity between the AI and sgACC in response to the pain of innocents resembling fair targets. The sgACC plays a pivotal role in modulating physiological arousal due to its extensive connections with brainstem and limbic systems (Dixon et al., 2017). Moreover, the sgACC is involved in processing a range of negative emotions, such as sadness, social exclusion, and anxiety (Drevets et al., 2008; Mayberg et al., 1999; Rotge et al., 2015). Thus, the heightened AI-sgACC connectivity might reflect increased pain-related visceral experience, facilitating emotional connection with innocents resembling fair targets. Second, we observed increased connectivity between the IPFC and sensorimotor areas in response to the pain of innocents resembling fair targets. The heightened connectivity was associated with increased reported pain intensity and greater altruistic sharing with innocents resembling fair (vs. unfair) targets. These findings suggest a top-down control mechanism for directing attention to pain-related sensory information and align with previous research indicating associations between sensorimotor responses to perceived pain and prosocial behaviors (Ma et al., 2011; Vickers et al., 2023).

Several limitations should be noted. First, the experiment did not include a control condition assessing empathic responses toward unrelated innocents or targets, which limits the ability to directly compare the effects of direct versus indirect social relationships and social structure. Second, repeated presentation of painful and non-painful

stimuli for each innocent may have introduced habituation effects. Although we varied the side of stimulation to mitigate this possibility, the limited number of facial identities likely reduced stimulus variability, potentially attenuating empathic responses over time. Third, different empathy paradigms are known to recruit distinct secondary neural networks (Lamm et al., 2011; Schurz et al., 2021; Zaki and Ochsner, 2012). While the current paradigm was designed to assess affective empathy through neural responses to others' pain, downstream altruistic behavior was also measured to capture potential concern-based reactions. Future studies incorporating direct measures of compassion and helping motivation are needed to further disentangle different components of empathy and their sensitivity to social structure (Batson, 2015; Weisz and Zaki, 2018; Zaki and Ochsner, 2012). Lastly, our interpretation of the fMRI results emphasizes emotion regulation, and this account is supported by converging evidence from activation patterns and brain-behavior correlations. Yet, the implicated regions—such as the dmPFC and TPJ—also support mentalizing (Arioli et al., 2021). These accounts are not mutually exclusive; rather, emotion regulation may operate via mentalizing processes, such as inferring others' intentions or group affiliations to justify reduced empathy (e.g., toward innocents resembling unfair targets). Future work using more targeted methods is needed to disentangle these related mechanisms.

Despite these limitations, our study provides the first evidence to uncover the neural signatures underlying the influence of social structure, constructed based on both self-other direct relations and other-other indirect relations, on human empathy and altruistic behaviors. Specifically, social structure exerts its influence on human empathy and altruism through brain systems that encompass distributed brain systems involved in emotion regulation and mentalizing (dmPFC, TPJ, vmPFC, and lPFC) and affective/sensorimotor processing (AI, PMC, M1/S1). These findings suggest that participants were more inclined to rely on their own pain experience when simulating the pain of individuals resembling fair targets, with a heightened focus on pain-related affective and sensorimotor information. In contrast, when simulating the pain of individuals resembling unfair targets, participants appeared to employ multiple emotion regulation strategies to attenuate their vicarious emotional responses. These findings offer novel insights on the flexible empathic and altruistic responses within the context of social structures. They enhance our understanding of how individuals navigate their social networks in the realms of emotional sharing and altruism, opening new avenues to explore the associations between social relationships and behaviors that go beyond direct self-other interactions.

Data and code availability

The results and the analysis code are available at https://github.com/SummerTian00/social_structure_modulating_pain_empathy. Because of the large size of the raw neuroimaging data, they will be available from the corresponding author on request.

CRediT authorship contribution statement

Xia Tian: Writing – original draft, Visualization, Formal analysis. **Zixin Zheng:** Writing – review & editing. **Renhui Li:** Writing – review & editing. **Yue-Jia Luo:** Resources, Funding acquisition. **Chunliang Feng:** Writing – review & editing, Methodology, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2025.121267](https://doi.org/10.1016/j.neuroimage.2025.121267).

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