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**Original Article**

# Boosting interpersonal emotion regulation through facial imitation: functional neuroimaging foundations

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**Empathic function, which is primarily manifested by facial imitation, is believed to play a pivotal role in interpersonal emotion regulation for mood reinstatement. To explore this association and its neural substrates, we performed a questionnaire survey (study l) to identify the relationship between empathy and interpersonal emotion regulation; and a task-mode fMRI study (study 2) to explore how facial imitation, as a fundamental component of empathic processes, promotes the interpersonal emotion regulation effect. Study 1 showed that affective empathy was positively correlated with interpersonal emotion regulation. Study 2 showed smaller negative emotions in facial imitation interpersonal emotion regulation (subjects imitated experimenter's smile while followed the interpersonal emotion regulation guidance) than in normal interpersonal emotion regulation (subjects followed the interpersonal emotion regulation guidance) and Watch conditions. Mirror neural system (e.g. inferior frontal gyrus and inferior parietal lobe) and empathy network exhibited greater activations in facial imitation interpersonal emotion regulation compared with normal interpersonal emotion regulation condition. Moreover, facial imitation interpersonal emotion regulation compared with normal interpersonal emotion regulation exhibited increased functional coupling from mirror neural system to empathic and affective networks during interpersonal emotion regulation. Furthermore, the connectivity of the right orbital inferior frontal gyrus–rolandic operculum lobe mediated the association between the accuracy of facial imitation and the interpersonal emotion regulation effect. These results show that the interpersonal emotion regulation effect can be enhanced by the target's facial imitation through increased functional coupling from mirror neural system to empathic and affective neural networks.**

*Key words*: interpersonal emotion regulation (IER); affective empathy; orbital IFG; imitation; mirror neural system (MNS).

## Introduction

Interpersonal emotion regulation (IER) refers to a set of social-communicative processes that can alter emotional experiences within the social context (Butler 2011; Zaki and Williams 2013; Hofmann 2014; Zaki 2020). Specifically, the key distinction of IER from self-emotion regulation lies in its emphasis on deliberate efforts made by one person (the regulator) to modify the emotional experience of the other person (the target). For instance, in the very beginning of our life, our emotions are often regulated by our parents. It forms the foundation for the cultivation of self-regulation in children (Morris et al. 2007), and serves as a crucial element of social support from friends and intimate partners (Butler and Randall 2013). Additionally, it assumes a pivotal function in the realm of professional management and psychotherapy (Grecucci et al. 2015). Importantly, several disorders, including depression and borderline personality disorder, are characterized by disruptions in IER function (Marroquín 2011; Hofmann 2014; Dixon-Gordon et al. 2015). Therefore, investigating how to improve IER effect as well as its neural substrates is worth considering.

The IER is theoretically conceptualized as a dynamic process between the target and the regulator, in which the target suffers negative emotions and the regulator assists in changing these emotions (Butler 2011; Reeck et al. 2015). Empathy has long been recognized as a critical factor in the dynamic IER process between the regulator and the target (Onoda et al. 2009; Butler 2011; Reeck et al. 2015). It refers to the ability to share the other person's affective state (affective empathy) and thoughts (cognitive empathy; Levy et al. 2019; Li et al. 2017). To be specific, empathy is a crucial ability for the regulator to accurately perceive the target's affective state and effectively select an appropriate emotion regulation strategy (Zaki 2020; Reeck et al. 2015). On the other hand, the target's level of empathy may influence their ability to perceive positive emotions from the regulator. It is easier for a person with high affective empathy to perceive others' emotions and mirror their emotional states (Sallquist et al. 2009; Walter 2012). As the target's affective state serves as a crucial indicator of the IER effect, their heightened affective empathy may facilitate the perception of the regulator's affective state, leading to a similar positive emotional state between them. Therefore, empathy not only facilitates the regulator to perform timely interpersonal regulation but also serves as a key moderator of the IER effect on the target (Butler 2011; Reeck et al. 2015). Enhancing the target's

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affective empathy may reasonably improve the IER effect. A direct investigation is, therefore, necessary to explore the association between affective empathy and the IER effect, as well as the neural substrates underlying this association.

Meanwhile, previous studies have demonstrated that imitating others' body language, such as facial expressions and movements, can effectively enhance one's affective empathy (Stel et al. 2009; Inzlicht et al. 2012; Walter 2012). Typically, researchers confirm the validity of individuals' elicited affective empathy responses toward others by imitating their facial expressions (Sonnby-Borgström 2002). Also, Braadbaart et al. (2014) reveal that the similarity of facial imitation correlates positively with empathic responses. This suggests that improving the target's facial imitation performance in response to the regulator would be highly beneficial for enhancing the target's capacity for affective empathy, thereby enhancing the IER effect. Therefore, the present study was designed to investigate whether enhancing the target's affective empathy via facial imitation could enhance the IER effect.

Indeed, fMRI studies have revealed that facial imitation is predominantly manifested through the activation of the mirror neural system (MNS; Wager et al. 2008; Jabbi et al. 2007; Kaplan and Iacoboni 2006; Shamay-Tsoory et al. 2009). The MNS that mainly includes the inferior frontal gyrus (IFG) and the inferior parietal lobe (IPL). IFG was initially identified in the F5 region of monkeys (Murata et al. 1997). In humans, IFG is automatically engaged as a neural mechanism when observing or imitating others' actions (Shamay-Tsoory et al. 2009). It has also been found that the MNS is the neural basis of empathy, with the activation of IFG being particularly critical for affective empathy (Shamay-Tsoory et al. 2009; Bekkali et al. 2021). For instance, Kaplan and Iacoboni (2006) instructed participants to watch precision grips action to fire MNS, revealing a positive correlation between measure of affective empathy and activation of IFG. In addition, a brain damage study demonstrates that the IFG-damaged patients exhibit reduced affective empathy compared with healthy individuals (Shamay-Tsoory et al. 2009). For emotion regulation, many studies have observed that the activations in IFG and IPL increase when participants engage in the reappraisal strategy (Wager et al. 2008; Ochsner et al. 2012; Zhao et al. 2021). Furthermore, the activation of IFG shows a positive correlation with measures of emotion regulation (Wager et al. 2008). Taken together, empathy and emotion regulation may share the same neural basis of MNS, it is necessary to examine the role of MNS in the association between empathy and IER.

Based on the aforementioned, our hypotheses were as below: first, a significant correlation exists between the target's affective empathy and IER; second, the facial imitation may improve the IER effect; third, the MNS may serve as an essential neural substrate for enhancing the IER effect through facial imitation. To test these hypotheses, a 2-step approach was employed. Study 1 utilized the basic empathy scale (BES) and the interpersonal regulation questionnaire (IRQ) to identify the association between the target's empathy and IER. Subsequently, study 2 employed a task-mode fMRI study to explore the neural substrates underlying the modulation of the IER effect by facial imitation. Initially, we assessed the activations of facial imitation IER (MIER) > normal IER (NIER) contrast to determine whether regions associated with empathy, particularly those related to the MNS, exhibited greater activations during the MIER condition. Then, we focused on MNS and employed it as the seed region in order to elucidate the functional connectivity among various cerebral regions that collaborate with the MNS. Therefore, the functional activity and functional connectivity of MNS could be the neural index of empathy to investigate the neural substrates underlying the relationship between empathy and IER.

# Materials and methods

## Study 1

### *Subjects*

For the first study, we recruited 112 healthy college students (55 females, 57 males; mean age = 21.89, SD = 2.71). All of them were right-handed, had normal or corrected-to-normal vision, and had no family history of psychiatric, neurological, or affective disorders. The study was approved by the local ethics committee of the University of Electronic and Scientific Technology of China, and informed consent was obtained from all subjects who also received financial compensation.

## Questionnaires

The present study used the IRQ and the BES to investigate the relationship between IER and the target's empathy. The IRQ consists of 2 subscales: Interpersonal Regulation Tendency (IRQ_T) subscale and Interpersonal Regulation Efficiency (IRQ_E) subscale. The IRQ_T measures one's tendency to engage in IER, whereas the IRQ_E assesses their effectiveness in perceiving IER (Williams et al. 2018). Meanwhile, the BES includes cognitive empathy subscale and affective empathy subscale. The cognitive empathy subscale measures one's ability to understand others' feelings, whereas the affective empathy subscale measures one's perception of others' emotions (Walter et al. 2012). To control the effects of anxiety, depression, and personal traits on IER, we conducted a regression analysis using the State-Trait Anxiety Inventory (STAI), Beck Depression Inventory (BDI), and Neuroticism Extraversion Openness Personality Inventory (NEO-PI) to control for these factors in our present results.

## Study 2

### *Subjects*

Fifty-five healthy college students (26 females, 29 males; mean age = 20.5, SD = 1.96) were recruited in study 2. All of them were right-handed, had normal or corrected-to-normal vision, and had no family history of psychiatric, neurological, or affective disorders. Same as that in study 1, the subjects also finished the IRQ, BES, STAI, BDI, and NEO-PI questionnaires. Two subjects were excluded from data analysis because of their head motion exceeded 2 mm or 2° during the MIER condition.

## IER task

The present IER task combined the previous fMRI tasks of IER and facial imitation (Carr et al. 2003; Kim and Hamann 2007; McRae et al. 2010; Mulej Bratec et al. 2015; Xie et al. 2016). The present task used a within-subjects design, including 3 conditions: NIER condition, MIER condition, and watch condition (Watch). The 3 conditions were performed by each subject in 3 different sessions. Each session consisted of 20 trials. Each trial began with a (i) 1-s fixation, followed by (ii) an instruction phase (4 s), which varied across conditions, subjects were guided on how to view the subsequent emotional pictures. In the NIER and Watch conditions, they were instructed to listen to the experimenter carefully. In the MIER condition, they were instructed to listen carefully and imitate experimenter's smile; (iii) a video clip (7 s), in which subjects were instructed on how to use the reappraisal strategy to reduce their negative emotions (NIER and MIER conditions), or watch the pictures (Watch condition); (iv) a jitter randomized from

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1 to 3 s; (v) an emotional picture appeared for 7 s. During picture presentation, subjects were required to memorize the instruction from the previous video clip in order to regulate their emotions (NIER/MIER) or experience their emotions (Watch); (vi) emotional rating on a 5-point scale from 0 = not negative at all to 4 = very negative (3 s). For MIER condition, the subjects needed to rate how similar the facial imitation is on a 5-point scale from 0 = not at all to 4 = very similar (3 s) after the emotional rating phase (see Fig. 1 for more details of the task).

The 60 emotional pictures were selected from the international affective picture system and open affective standardized image set (Benedek 2017; the picture numbers shown in Supplementary Materials). The 60 pictures were randomly assigned to the MIER, NIER, or Watch conditions, with no significant difference in arousal [$F$ (2, 62) = 0.182, $P$ = 0.834] and valence [$F$ (2, 62) = 1.603, $P$ = 0.210] across the 3 conditions.

In the NIER and MIER conditions, the experimenter helped the subjects decrease their negative emotions through distancing or positive reappraisal strategies by using phrases such as “Don’t worry, the scene is not related to you; Don’t worry, the rescue teams are on their way.” Therefore, the current conditions could establish a social context (Reeck et al. 2015; Xie et al. 2016). The distancing strategy reduces negative emotions by using a detached perspective, which can increase the distance between the subject and negative scene, thereby decreasing their self-involvement (McRae et al. 2012). The positive reappraisal strategy aims to guide subject toward a positive perspective when facing negative emotions (Ochsner et al. 2012). In the Watch condition, subject was instructed to look at the picture and feel their emotions, with a phrase such as “Experience your feelings when looking at the picture.” This condition matched the “look” condition in previous neuroimaging studies on cognitive reappraisal (Kim and Hamann 2007; McRae et al. 2010; Ochsner et al. 2012; Mulej Bratec et al. 2015). A block-design method was used, where the 3 conditions were distributed separately in 3 sessions. The order of the 3 conditions was counterbalanced across the subjects. Every session has 20 trials, which resulted in 60 unique instruction video clips for 3 conditions. Before the task, we informed the subjects that we had a monitor, which could check their imitation performance during scanning. If they did not perform imitation, a portion of their financial compensation would be deducted. Actually, we did not have this monitor, and this statement was made solely to ensure that the subjects followed the imitation instruction. All participant instructions can be found in the Supplementary Materials.

In the present study, the subjects were the targets and the experimenter (a female PhD student in psychology) acted as the regulator. Prior to the task, all of the targets received instructions on how to decrease their negative emotions by the regulator. Then, the targets were informed that the regulator would guide them in regulating their negative emotions through short video clips during the formal fMRI experiment. Once the targets had understood all the procedures, the formal experiment commenced.

## Statistical analysis

First, we employed 1-way analysis of variance (ANOVA) on the behavioral data to examine the differences in emotional rating across the 3 conditions and determine whether facial imitation influences the IER effect, which was computed by the reduced emotion intensity of the targets. For the neural data, we calculated the functional activity and functional connectivity in MIER and NIER conditions to explore the neural substrates of empathy and IER. As the MNS is the key system for empathy, and we manipulated imitation to enhance empathy, MNS was employed as a neural indicator of empathy.

During the present task, the video phase involved the empathic process between the target and the regulator, whereas the execution phase (emotional picture phase) was the executive process of emotion regulation. We compared the MIER and NIER conditions during the IER execution phase to describe the neural activation of the enhancement of the IER effect after facial imitation. Meanwhile, we tested whether empathy network, particularly the MNS, exhibits stronger functional activity in MIER condition at video phase. Then, the MNS was employed as the seed region for whole-brain functional connectivity analysis, aiming to depict the functional coupling profiles among different empathy-related cerebral regions. All the degrees of freedom were corrected by the Greenhouse–Geisser method, and Bonferroni correction was used in the post hoc test and the main effect. The statistical analysis was performed in Statistical Product Service Solutions software (SPSS 20.0).

## Data acquisition

The fMRI data were collected on a 3.0-T GE Discovery MR750 system (General Electric Medical System, Milwaukee, WI, United States), with an 8-channel phased-array head coil. The fMRI data were obtained using a single-shot simultaneous multi-slice or multiband gradient-echo EPI sequence with the following parameters: echo time = 30 ms, repetition time = 2000 ms, flip angle = 90°, spacing between slices = 3 mm, field of view = 240 × 240 mm, acquisition matrix = 64 × 64, slice thickness = 3 mm, slice number = 42.

## Data preprocessing

The preprocessing of fMRI data was carried out with Dpabi (V3.1) toolbox (http://www.rfmri.org/dpabi) on Matrix laboratory software (MATLAB 2018a, https://www.mathworks.cn/en/products/matlab). The processes are as follows: (i) removed first 5 time points; (ii) sliced timing correction; (iii) realignment; (iv) spatial normalization by EPI template; (v) smoothed with a Gaussian kernel (FWHM = 8 mm).

## Activation analysis

The preprocessing data were fed into a General Linear Model for the first-level analysis of each subject in each condition based on blood oxygen-level-dependent signal. The onset time of emotional picture signals the IER execution phase and the video onset served as the empathic processes between the target and the regulator. The 2 onsets were accessed as the regressor-of-interest. Additionally, onsets of other stimuli (i.e. fixation cross, instruction, and rating phases) and the 6 head motion parameters as regressors-of-no-interest to remove. All regressors were convolved with the hemodynamic response function, and high-pass filter was 128 s. Then, the individual first-level results were entered into group-level analysis. The activations were the contrast of MIER > NIER and MIER < NIER in IER execution phase and video phase. All the contrast were corrected at voxel-wise FDR correction of $P < 0.005$. The activation analysis was carried out with Statistic Parametric Mapping 12 toolbox on MATLAB 2018a (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/).

## Functional connectivity

As the key regions of MNS are IFG and IPL, we selected the orbital frontal inferior gyrus (orb IFG), triangle frontal inferior gyrus (tri IFG), operculum frontal inferior gyrus (oper IFG), and IPL as the regions of interest (ROI) under the automated anatomical labeling

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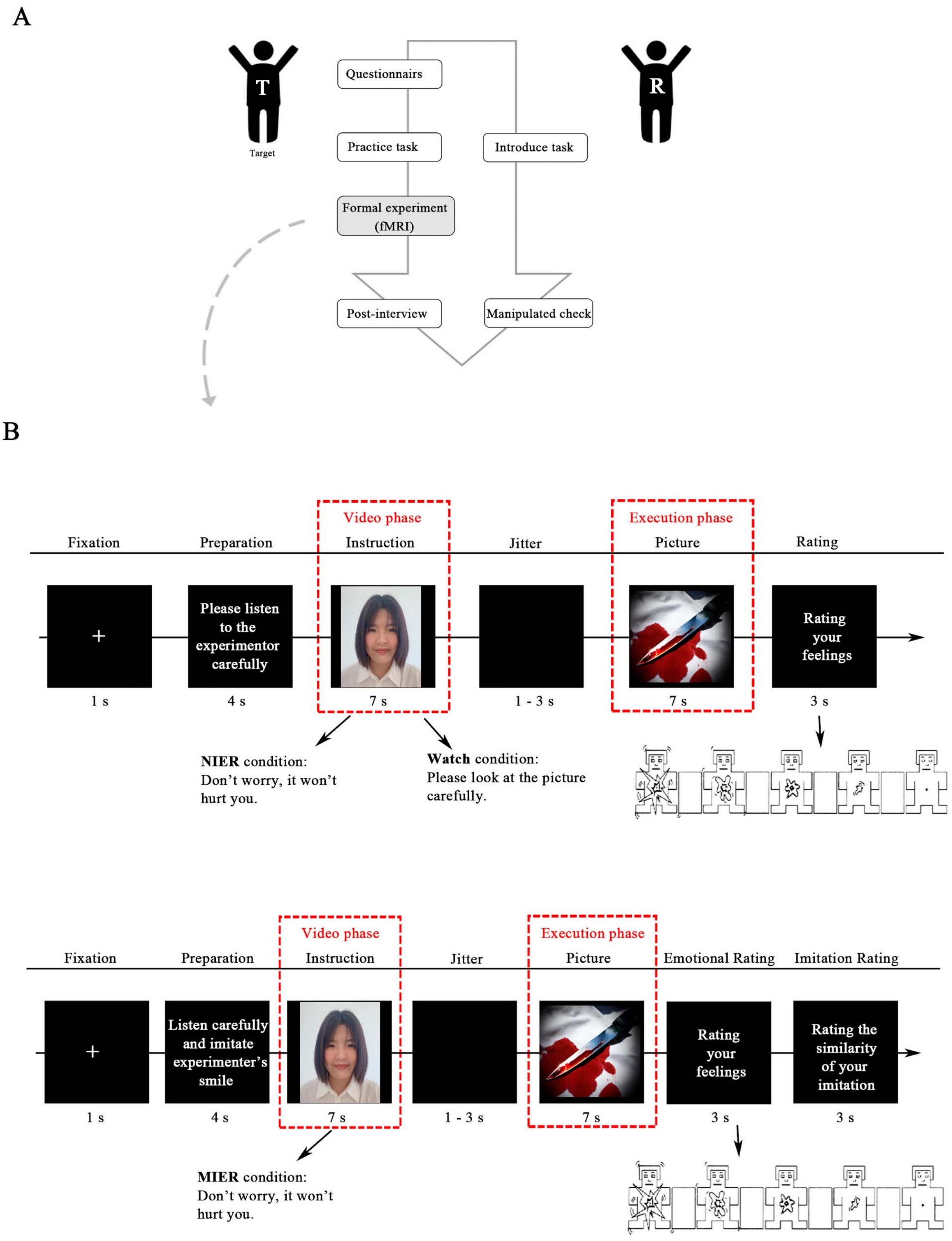


**Fig. 1.** a) The study timeline was as follows: The subjects were the targets, and the experimenter acted as the regulator to guide them in downregulating their negative emotions. First, the targets completed all questionnaires. Then, the regulator introduced the IER task. Once the targets had understood all the procedures, the formal experiment commenced. After the formal experiment, a post-interview was conducted to verify that the IER process had been successfully induced in the present study. b) The schematic of the IER task. The task included 3 conditions: the NIER condition, the MIER condition, and the watch (Watch) condition.

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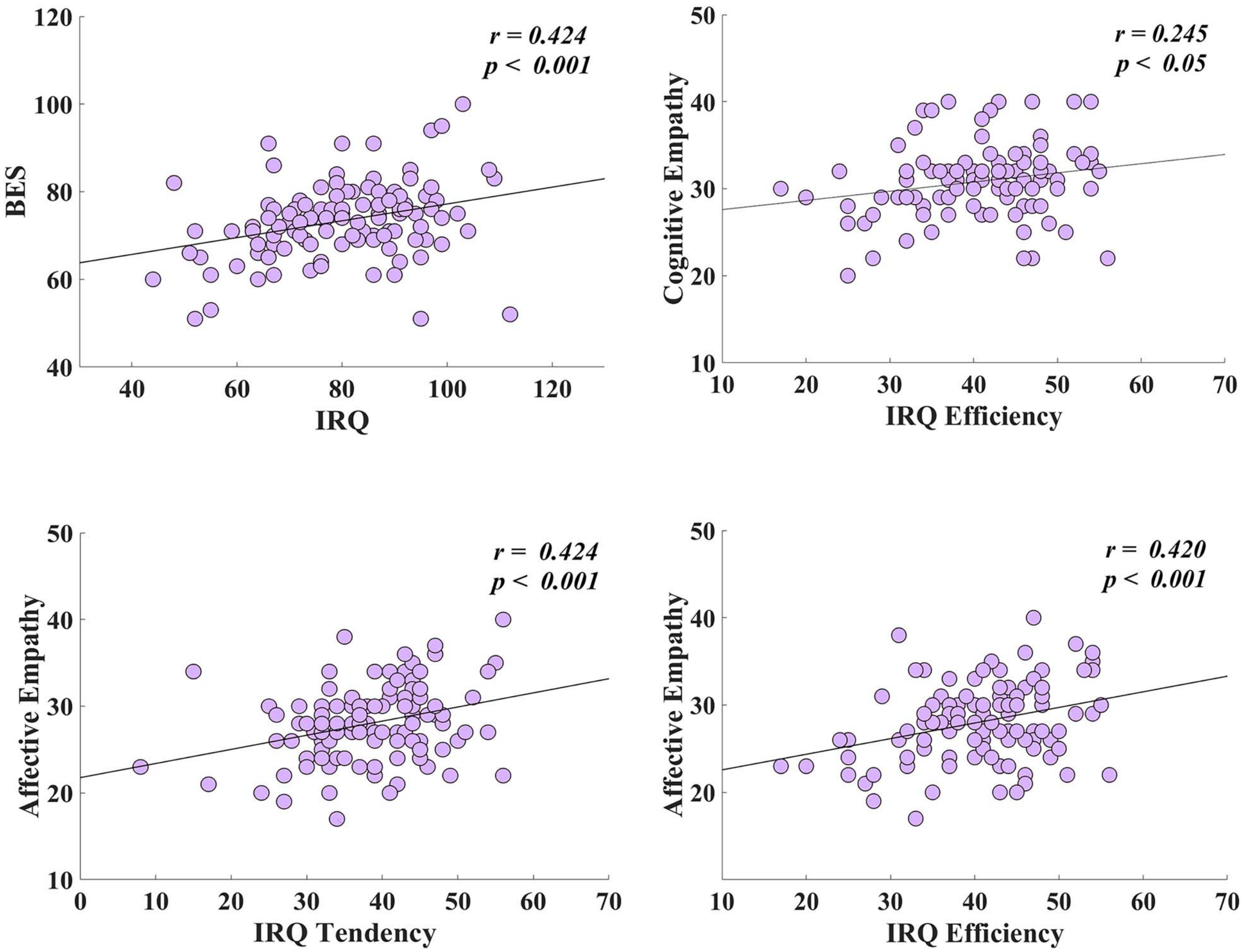


**Fig. 2.** The correlation results of IRQ and BES after regressed personality (NEO-PI scale), depression level (BDI), and trait of anxiety (STAI) scores.

atlas. Then, we obtained the ROI (89) ∗ condition (2, NIER/MIER) ∗ subjects (53) Pearson correlation coefficient ($r$-value) matrix of the 8 ROI, respectively. The functional connectivity was estimated by calculating Fisher's z-value of Pearson correlation coefficient.

Functional connectivity was computed based on multiple regression analyses. Signals were extracted by averaging the time courses from each ROI. To reduce the effects of physiological signals and task design noise (It may cause fake correlation), 6 (in NIER condition) or 7 (in MIER condition) covariates (i.e. fixation, rating) and 6 motion parameters were added to the regression analysis. Then we used bilateral IFG and IPL as the seed regions to calculate whole-brain functional connectivity in ROI wise. Functional connectivity serves as the index of the relationship between the empathy and IER, and 2 factors (conditions × functional connectivity) repeat measure ANOVA were conducted in current study. The functional connectivity analysis was carried out with Dpabi (V3.1) toolbox on MATLAB 2018a (Mathworks, MA, USA).

# Results

## Study 1

Correlations among IRQ, BES, and their subscales were computed after controlling the measures of STAI, BDI and NEO-PI scales. The results showed a strong positive relationship between IRQ and BES scores ($r = 0.424$, $P < 0.001$; Fig. 2). Affective empathy had significant positive correlations with IRQ_E ($r = 0.420$, $P < 0.001$) and IRQ_T ($r = 0.424$, $P < 0.001$). The cognitive empathy had positive correlation with IRQ_E ($r = 0.245$, $P < 0.05$) only.

## Study 2

### *Manipulation check*

Post-experimental interview verified that all subjects followed the experimenter's guidance. They reported lower negative feelings in NIER and MIER conditions than in Watch condition, which implied successful induction of IER in the present study.

### Behavioral results

A 1-way ANOVA was conducted on the emotional rating score (0 [not negative at all], −4 [very negative]) with NIER, MIER, and Watch conditions. The main effect of conditions on emotional rating was significant [$F(2, 87) = 12.149$, $P < 0.001$]. The MIER condition had the lowest emotional rating among the 3 conditions (Fig. 3). The mean emotional rating of 3 conditions was Watch = 2.55 ± 0.7341; NIER = 2.12 ± 0.58; MIER = 1.77 ± 0.51. Meanwhile, the IER enhancement effect of NIER–MIER emotional rating had a significant positive correlation with imitation rating ($r = 0.285$, $P = 0.044$).

### Activation results

We constructed the MIER > NIER contrast in the video phase, revealing increased activations in MNS (bilateral IFG, IPL), dorsolateral prefrontal cortex (DLPFC), dorsomedial prefrontal cortex (DMPFC), precuneus (PCUN), temporal parietal junction (TPJ),

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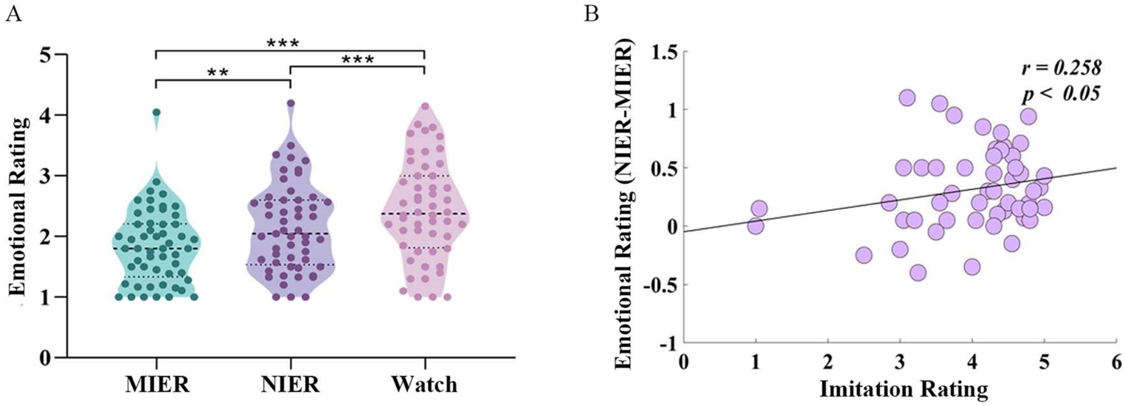


**Fig. 3.** a) The emotional rating of NIER, MIER, and Watch conditions after the subjects regulated their negative emotion or just watched the pictures with the guidance of the regulator. b) The correlation between imitation rating and the emotional rating of NIER–MIER conditions.

insula (INS), and thalamus (THA; Fig. 4 and Table 1). The activations largely overlapped with crucial regions of the empathy identified in previous studies (Walter 2012; Haakon 2012). However, the video phase showed stronger activations in the bilateral middle temporal gyri (MTG), and the right inferior/superior temporal gyri (STG) during NIER compared with MIER conditions.

In the execution phase, the comparison of MIER > NIER showed stronger activations in MNS, DLPFC, DMPFC, amygdala (AMG), INS, etc. The contrast of MIER < NIER exhibited pronounced activations in the left middle temporal and the right STG (see Table 2).

## Functional connectivity

The 2-factor repeated measure ANOVA of the connectivity of bilateral orb IFG to whole brain (89 ROIs), with ROI ∗ conditions (2, NIER/MIER) as factors, showed significant main effect of conditions (left: [$F$ (1, 52) = 15.838, $P < 0.05$], right: [$F$ (1, 52) = 20.824, $P < 0.001$]), with larger connectivity of bilateral orb IFG to whole brain in MIER condition than in NIER condition. The interaction effects on the connectivity of bilateral orbital IFG to whole brain (left: [$F$ (12, 630) = 1.787, $P < 0.05$], right: [$F$ (13, 680) = 2.052, $P < 0.05$] were significant. Further analysis showed stronger connectivity of bilateral orbital IFG to empathy network (e.g. ventromedial prefrontal cortex [VMPFC], DMPFC, INS, and TPJ) and affective-generating network including AMG and THA in MIER condition than in NIER condition (Fig. 5). Additionally, there was no significant interaction effect in bilateral tri IFG and oper IFG to whole brain.

The 2-factor repeated measures ANOVA of the connectivity of bilateral IPL to whole brain, with conditions (NIER/MIER) and ROI (89 ROIs) as factors, showed significant main effect of conditions (left: [$F$ (1, 52) = 20.983, $P < 0.001$], right: [$F$ (1, 52) = 14.126, $P < 0.001$]), with enhanced connectivity of bilateral IPL to whole brain in MIER condition than in NIER condition. Additionally, the condition by ROI interaction effects on the connectivity of bilateral IPL to whole brain (left: [$F$ (14, 734) = 3.686, $P < 0.001$], right: [$F$ (16, 834) = 4.690, $P < 0.001$]) was significant. The post hoc pairwise comparison showed stronger connectivity of bilateral IPL to empathy network (e.g. VMPFC, DMPFC, INS, and TPJ) and affective-generating network including AMG and THA in MIER condition than in NIER condition (Fig. 5).

## Mediation results

The mediation analysis was performed on a bootstrap test using the standard 3-variable path model (Menatti et al. 2015; Wager et al. 2008; Wang et al. 2020). We tested the relationship among imitation rating, emotional rating of NIER-MIER and the connectivity of MNS to whole brain under MIER-NIER. The results showed that the connectivity of right orb IFG to right rolandic operculum lobe (ROL) mediated the relationship between imitation rating and emotional rating of NIER–MIER (indirect path a = −0.1725; indirect path b = −0.1470, total relationship c = 0.0914, direct path c' = 0.0660; 95% bootstrap confidence interval (CI) = [0.0012, 0.0803]; effect size = 27.79%; Fig. 6). Zero does not appear in the CI, which illustrates a statistically significant mediation effect for the mediating factor.

# Discussion

The current study 1 described the association between the target's empathy and IER. Based on the association, we tried to manipulate the empathy of the target by facial imitation and attempted to enhance the IER effect under a task-mode fMRI study. The results demonstrated that (i) the target's empathy was positively correlated with IER; (ii) the activations of empathy network (e.g. MNS, VMPFC, TPJ, INS, and PCUN) were more prominent in MIER condition than in NIER condition; (iii) the emotional rating in MIER was the lowest among all conditions (MIER/NIER/Watch); (iv) the connectivity of MNS to empathy network and affective-generating system was more pronounced in MIER condition than in NIER condition; (v) the mediation result showed that the connectivity of the right orb IFG-ROL significantly mediated the association between the accuracy of facial imitation and enhanced emotion-regulatory effect during MIER compared with NIER conditions.

## The positive relationship between IER and empathy of the target

Study 1 demonstrated that the target's empathy had a significant positive relationship with IER. Specifically, the affective empathy was positively correlated with IER tendency and efficiency. Affective empathy is elicited by perceiving the other person's affective state and activating an isomorphic affective state in oneself (Walter 2012; Jami et al. 2023). During the IER process, a better ability for affective empathy may imply that the target finds it easier to perceive the regulator's emotional state, as they consistently display positive emotions toward the target. This positive perception of emotions can help the target alleviate their negative emotion arousal. Moreover, improving affective empathy could lead to a more efficient outcome in IER, which may also increase the target's tendency to use IER (Decety and Jackson 2004; Zaki 2020). Therefore, this association may provide a way to

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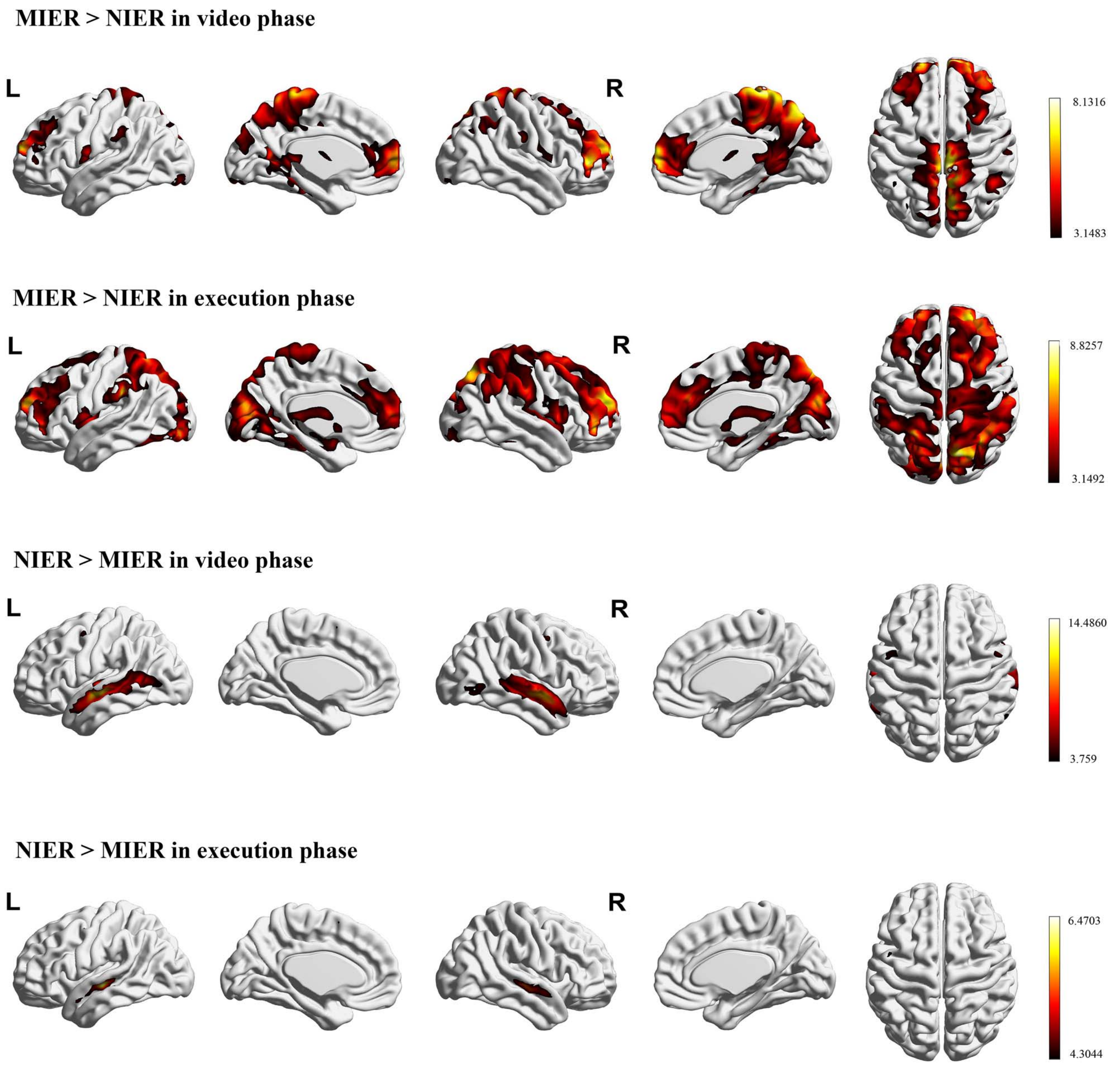


**Fig. 4.** Brain regions activated by MIER and NIER comparison in the video phase and execution phase. The *t*-values were corrected by FDR at $P < 0.005$.

improve IER through enhancing the affective empathy of the target.

## Facial imitation enhanced empathy of the target during the IER process

Meanwhile, study 2 demonstrated that facial imitation induced more pronounced activations of empathy network such as MNS, VMPFC, and affective-generating system in IER process. In general, the MNS codes for affective stimuli and directs the body to execute the same movement with a specific goal in mind (i.e. facial imitation), thereby providing an access to shared emotional experiences and establishing a robust foundation for empathy (Iacoboni 2009; Bekkali et al. 2021). This improved affective resonance, as an important part of empathic processes, laid a further basis for potential improvement of IER effects the target obtained from the regulator. Additionally, temporal cortex showed stronger activation in NIER than in MIER conditions during the video phase, which is primarily involved in cognitive empathy processes for understanding and sharing other people's feelings (Walter 2012). Thus, facial imitation may enhance affective empathy rather than cognitive empathy. Taken together, these findings suggest that facial imitation improved the target's affective empathy, and elicited a stronger emotional connection with the regulator.

On the other hand, functional connectivity of neural activation is used to evaluate the functional coupling among different cerebral regions that work together. A strengthened connection implies a stronger functional association between these regions (Friston et al. 1997; Gao et al. 2021). The functional connectivity between the MNS and other empathy network was further strengthened in MIER condition, indicating an enhanced ability for empathy through collaboration between the MNS and empathy network. Furthermore, numerous researchers emphasize that the core affective empathy network involves INS and VMPFC. Nevertheless, some studies have brought to light a distinct neural pathway for negative affective empathy and positive affective empathy. The activation of the INS is

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Table 1. Brain regions activated in the video phase of MIER < NIER and MIER > NIER comparisons in ROI based at FDR $P < 0.005$ level.

| | VS | MNI | | | T | | VS | MNI | | | T |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | x | y | z | | | | x | y | z | |
| **MIER > NIER comparison** | | | | | | | | | | | |
| IFG_L | 144 | −21 | 36 | −6 | 3.9202 | IFG_R | 227 | 39 | 45 | 0 | 7.6290 |
| VMPFC L | 94 | 0 | 60 | 0 | 6.6425 | VMPFC_R | 111 | 3 | 63 | 0 | 6.6425 |
| DLPFC_L | 581 | −24 | 57 | 18 | 5.5759 | DLPFC_R | 863 | 39 | 45 | 3 | 7.6211 |
| DMPFC_L | 597 | −18 | 60 | 18 | 7.755 | DMPFC_R | 870 | 12 | 63 | 12 | 8.1316 |
| PCL_L | 602 | −3 | −36 | 75 | 6.8396 | PCL_R | 579 | 6 | −39 | 72 | 7.757 |
| | | | | | | SMA_R | 120 | 6 | −21 | 72 | 5.9584 |
| | | | | | | IPL_R | 161 | 45 | −51 | 48 | 5.185 |
| SPL_L | 89 | −6 | −81 | 51 | 4.742 | SPL_R | 258 | 9 | −81 | 54 | 7.7212 |
| PCUN_L | 643 | −3 | −54 | 69 | 6.9574 | PCUN_R | 787 | 6 | −78 | 54 | 7.6114 |
| SMG_L | 69 | −57 | −39 | 36 | 4.3824 | SMG_R | 84 | 51 | −24 | 27 | 4.876 |
| CUN_L | 186 | −9 | −93 | 36 | 5.4086 | CUN_R | 182 | 12 | −84 | 48 | 6.1127 |
| | | | | | | TPJ_R | 131 | 42 | −57 | 51 | 4.5181 |
| FFG_L | 140 | −36 | −18 | −30 | 5.2513 | FFG_R | 113 | 36 | −27 | −24 | 5.2738 |
| LING_L | 102 | −27 | −69 | 0 | 4.9169 | LING_R | 132 | 15 | −51 | 6 | 5.271 |
| CAL_L | 181 | −21 | −54 | 9 | 6.8383 | CAL_R | 225 | 24 | −48 | 12 | 6.6489 |
| ACC_L | 205 | 0 | 54 | 0 | 5.8932 | ACC_R | 258 | 15 | 48 | 21 | 5.5754 |
| MCC_L | 144 | −12 | −42 | 42 | 5.4945 | MCC_R | 233 | 9 | −30 | 42 | 6.7228 |
| | | | | | | ROL_R | 112 | 39 | −9 | 24 | 4.753 |
| **MIER < NIER comparison** | | | | | | | | | | | |
| MTG_L | 743 | −58 | −11 | −4 | 12.62 | MTG_R | 416 | 59 | −14 | −8 | 8.7606 |
| | | | | | | ITG_R | 56 | 47 | −67 | −3 | 5.3839 |
| | | | | | | SPTG_R | 102 | 54 | 5 | −11 | 9.6163 |

Brain region abbreviation. VS, voxel size; PCL, paracentral lobe; SMA, supplementary motor area; SMG, supramarginal gyrus; CUN, cuneus; CAL, calcarine lobe; ACC, anterior cingulate cortex; MCC, middle cingulate cortex; ITG, inferior temporal gyrus; SPTG, superior pole temporal gyrus.

predominantly associated with negative affective empathy (especially for pain), whereas the VMPFC exhibits a significant association with positive affective empathy (Lamm et al. 2015; Morelli et al. 2015; Riva et al. 2018). In line with prior research, our findings indicated that the VMPFC was activated when the target imitated the regulator's smile. However, there was no significant activation of the INS cortex after FDR correction. Crucially, as a pivotal component of the human brain's reward system, the VMPFC plays a crucial role in encoding positive affective stimuli across diverse modalities such as smile (Mobbs et al. 2009). In the present results, VMPFC may intricately work with the affective-generating system, including the fusiform gyrus (FFG), lingual (LING) gyrus, and caudate (CAU) nucleus, to evoke a stronger positive affective empathy link between the target and the regulator. Taken together, facial imitation improved the target's affective empathy, indicating that the target exhibited a more robust affective empathic response toward the regulator.

## Facial imitation improved IER effect

As expected, the behavioral results exhibited that emotional rating was lower in MIER compared with NIER and Watch conditions. This suggested that the facial imitation lightened the negative experience, and improved the IER effect at behavioral level. During the execution phase, MIER condition was associated with greater activations in the medial/lateral prefrontal cortex, orbitofrontal cortex, IPL, superior parietal lobe (SPL), TPJ, and PCUN in comparison with NIER condition. This prefrontal–parietal network is well known for its critical role in cognitive emotion regulation and top-down cognitive control (Ochsner et al. 2012; Buhle et al. 2014). Thus, these data suggest that MIER may have drawn more resources from the general cognitive control network. On the other hand, MIER recruited activity of the TPJ, dorsomedial PFC, and PCUN, which were typically involved in complex social functions required for successful social interactions (Amodio and Frith 2006; Cavanna and Trimble 2006; Carter and Huettel 2013). Meanwhile, the comparison of NIER > MIER in execution phase showed stronger activations of MTG and STG, 2 cortical regions known for the roles in semantic perception (Binder et al. 2009). Therefore, these results suggest that MIER should have recruited more cognitive control and social-interactive processes to enhance downregulation of negative emotions, whereas NIER relied more on semantic perception and understanding, during IER.

Furthermore, the neural findings revealed that in MIER condition, the connectivity between the MNS and affective-generating network (i.e. ROL) was significantly stronger than that observed in NIER condition. This connectivity may indicate that the empathy network is directly oriented toward the affective-generating network to enhance the IER effect. This assumption is supported by the mediation result that the connectivity of the right orb IFG-ROL mediated the association between imitation rating and the enhancement of the IER effect. The ROL plays a pivotal role in implicating affective responses to external stimuli and exquisitely attunes to specific forms of affective discrimination (Chen et al. 2021). A neural investigation of depression disorder reveals a positive correlation between ROL and depressive disorder, suggesting that the ROL may be a potential region for noninvasive brain stimulation treatment of depressive disorder (Zhang et al. 2020). In conjunction with prior research, the connectivity of the orb IFG-ROL may indicate that affective state modulation occurs via empathy network. Crucially, this pathway significantly mediated the accuracy of facial imitation and the enhancement of the IER effect. Collectively, these results provide novel behavioral and neural evidence that facial imitation is a potentially effective way to improve the IER effect.

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**Table 2.** Brain regions activated in the execution phase of MIER < NIER and MIER > NIER comparisons in ROI based at FDR $P < 0.005$ level.

| | VS | MNI | | | T | | VS | MNI | | | T |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | x | y | z | | | | x | y | z | |
| **MIER > NIER comparison** | | | | | | | | | | | |
| IFG_L | 1,092 | −45 | 45 | −3 | 5.7727 | IFG_R | 1,162 | 39 | 45 | −3 | 7.5724 |
| OFG_L | 176 | 12 | 60 | 0 | 5.1733 | OFG_R | 192 | 12 | 60 | 0 | 5.4132 |
| DLPFC_L | 1,107 | −24 | 57 | 18 | 6.7313 | DLPFC _R | 1,290 | 24 | 57 | 27 | 7.6768 |
| DMPFC_L | 1,530 | −24 | 57 | 21 | 7.1630 | DMPFC _R | 1,573 | 24 | 57 | 18 | 7.4946 |
| ROL_L | 288 | −48 | 0 | 9 | 5.3800 | ROL_R | 375 | 54 | 6 | 9 | 6.3445 |
| SMA_L | 560 | −12 | 24 | 60 | 4.3018 | SMA_R | 634 | 15 | 18 | 66 | 6.0275 |
| PCL_L | 372 | −9 | −21 | 72 | 5.2285 | PCL_R | 198 | 9 | −33 | 72 | 5.1884 |
| IPL_L | 678 | −24 | −66 | 45 | 57,849 | IPL_R | 414 | 42 | −51 | 48 | 6.4109 |
| SPL_L | 588 | −27 | −57 | 66 | 7.0533 | SPL_R | 586 | 12 | −75 | 54 | 8.5769 |
| PCUN_L | 1,017 | −27 | −60 | 6 | 5.2696 | PCUN_R | 875 | 12 | −78 | 57 | 8.0669 |
| TPJ_L | 325 | −30 | −54 | 36 | 4.3620 | TPJ_R | 482 | 33 | −63 | 45 | 7.4660 |
| CUN_L | 400 | 3 | −84 | 18 | 6.9039 | CUN_R | 434 | 21 | −78 | 48 | 7.2717 |
| SMG_L | 338 | −57 | −33 | 30 | 7.3448 | SMG_R | 541 | 57 | −24 | 39 | 6.2872 |
| IOG_L | 245 | −36 | −90 | −9 | 6.5842 | IOG_R | 276 | 30 | −96 | −12 | 4.4984 |
| MOG_L | 837 | −27 | −78 | 0 | 6.7949 | MOG_R | 569 | 30 | −60 | 39 | 7.2355 |
| SOG_L | 394 | −15 | −84 | 6 | 6.3325 | SOG_R | 421 | 30 | −63 | 42 | 7.5052 |
| CAL_L | 623 | −6 | −84 | 15 | 6.8834 | CAL_R | 542 | 24 | −72 | 6 | 8.0346 |
| LING_L | 658 | −24 | −72 | 0 | 7.1944 | LING_R | 672 | 64 | −72 | 3 | 7.8715 |
| FFG_L | 568 | −27 | −72 | −3 | 7.5103 | FFG_R | 575 | 27 | −75 | 0 | 6.7257 |
| ITG_L | 305 | −45 | −39 | −21 | 5.3646 | ITG_R | 272 | 54 | −42 | −21 | 5.4178 |
| SPTG_L | 160 | −21 | 6 | −18 | 4.7481 | SPTG_R | 98 | 21 | 9 | −18 | 4.9516 |
| INS_L | 535 | −36 | −3 | 0 | 5.9573 | INS_R | 506 | 33 | −15 | 9 | 5.6127 |
| AMG_L | 59 | −27 | 0 | −18 | 4.8760 | AMG_R | 69 | 30 | 0 | −12 | 5.4418 |
| CAU_L | 276 | −15 | −9 | 21 | 5.8737 | CAU_R | 281 | 18 | −15 | 21 | 6.7818 |
| ACC_L | 409 | 0 | 39 | 24 | 5.6344 | ACC_R | 391 | 6 | 39 | 24 | 6.2328 |
| MCC_L | 616 | 0 | 30 | 33 | 4.5288 | MCC_R | 593 | 9 | −27 | 36 | 4.9570 |
| PCC_L | 101 | −15 | −45 | 12 | 4.6083 | PCC_R | 79 | 12 | −39 | 9 | 3.9611 |
| HIP_L | 267 | −30 | −6 | −21 | 4.7350 | HIP_R | 281 | 30 | −6 | −15 | 4.8762 |
| PAL_L | 81 | −27 | −9 | −3 | 4.5801 | PAL_R | 76 | 30 | −9 | −3 | 5.4363 |
| PHIP_L | 211 | −21 | 3 | −21 | 4.3694 | PHIP_R | 261 | 21 | 6 | −18 | 4.7592 |
| PUT_L | 306 | −33 | −3 | 0 | 5.9783 | PUT_R | 322 | 33 | −9 | −3 | 5.9341 |
| THA_L | 313 | −12 | −9 | 18 | 5.7816 | THA_R | 307 | 18 | −15 | 18 | 7.4069 |
| **MIER < NIER comparison** | | | | | | | | | | | |
| MTG_L | 166 | −59 | −16 | −4 | 6.2397 | STG_R | 149 | 54 | −15 | −5 | 5.6909 |

Brain region abbreviation. VS, voxel size; OFG, orbital frontal cortex; PCL, paracentral lobe; SMA, supplementary motor area; CUN, cuneus; SMG, supramarginal gyrus; IOG, inferior occipital gyrus; MOG, middle occipital gyrus; SOG, superior occipital gyrus; CAL, calcarine lobe; ITG, inferior temporal gyrus; SPTG, superior pole temporal gyrus; ACC, anterior cingulate cortex; MCC, middle cingulate cortex; PCC, posterior cingulate cortex; HIP, hippocampus; PAL, pallidum; PHIP, parahippocampus; PUT, putamen.

## Limitation

Although the current study provides insight into the relationship between empathy of the target and the IER effect, some limitations should be acknowledged. First, the present study focused on the relationship between affective empathy and IER. However, study 1 also demonstrated a significant association between cognitive empathy and IER, which should be further explored in future studies (Cui et al. 2022). Second, the current study primarily relied on fMRI results to illustrate changes in empathy following facial imitation. It is important to consider other more direct index to describe the changing of empathy, such as combining self-rating and third-perspective rating of empathy by the experimenter, in future investigations to enrich our understanding of empathy and IER. Furthermore, because of the limited temporal resolution of fMRI, the study faced challenges in precisely characterizing the swiftly evolving process of IER. Therefore, future investigations could explore multiple modalities to delve deeper into the intricate interplay between empathy and IER. These noteworthy findings, despite their limitations, provide unique insights into the underlying cognitive and neural mechanisms that support the empathic effects on IER.

## Conclusion

In summary, the behavioral and neural findings of this study support the hypotheses that target's empathy is positively related to the IER effect. In particular, facial imitation as an important facet of empathy enhances the IER effect. This modulation effect is realized by the collaborative functioning of MNS, empathy network (e.g. VMPFC, TPJ, INS), and affect-generation network (AMG, THA, ROL). Specifically, MIER compared with NIER is associated with greater activations in MNS and empathy-related network (e.g. vmPFC, TPJ, INS). In addition, increased functional coupling from MNS to empathic and affect-generation networks plays an important role in the occurrence of the above MIER effects. These findings provide implications on how to amplify the IER effects and apply them to clinical intervention of affective disorders such as depression. As such, further studies need to investigate the

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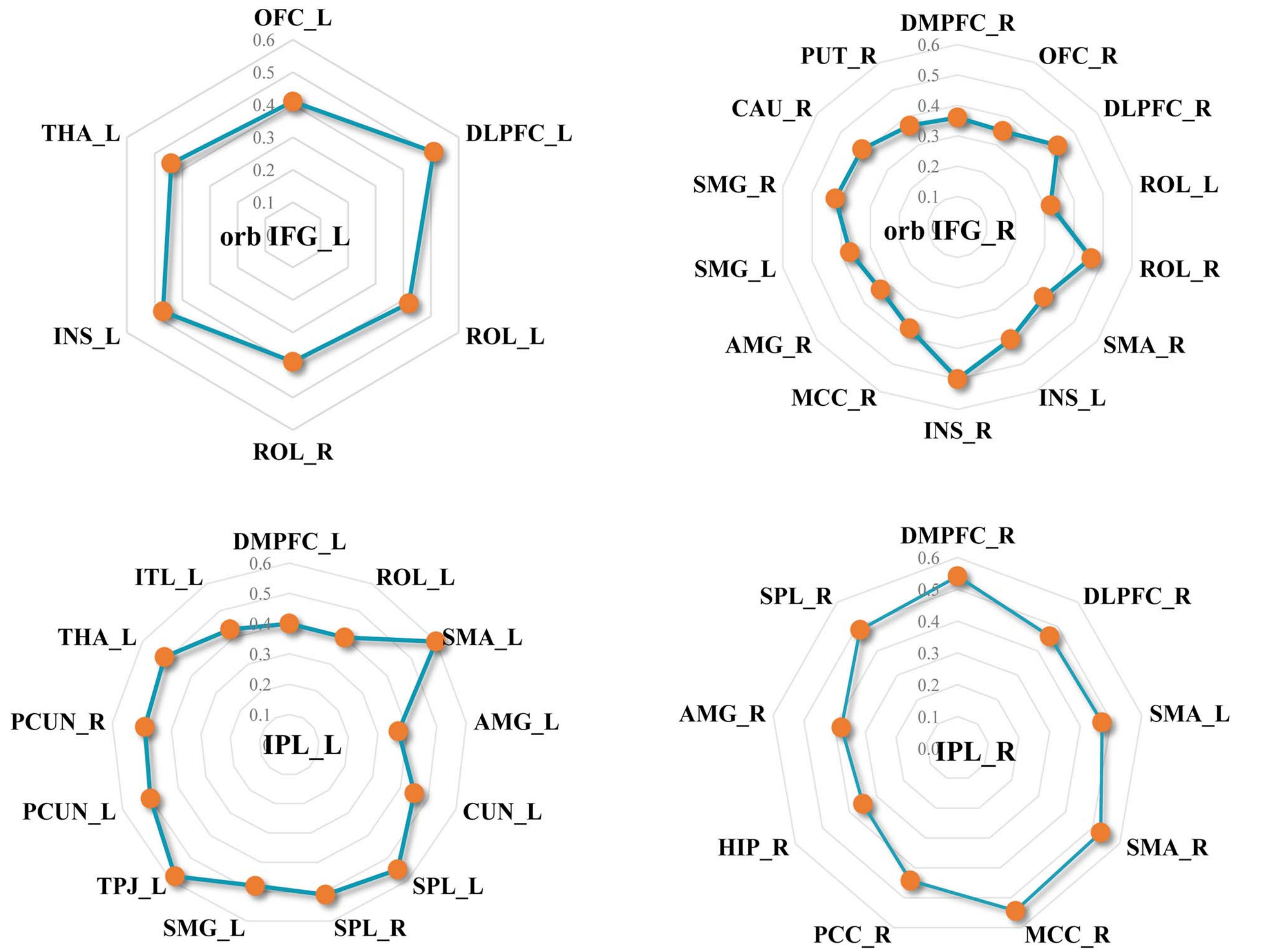


**Fig. 5.** The significant connectivity between the MNS (IFG, IPL) and whole brain in the MIER–NIER conditions. The significant connectivity was corrected by family-wise error at $P < 0.05$. Brain region abbreviation: OFC, orbital frontal cortex; SMA, supplementary motor area; SMG, supra marginal gyrus; CUN, cuneus; PUT, putamen; HIP, hippocampus; MCC, middle cingulate cortex; PCC, posterior cingulate cortex; ITG, inferior temporal gyrus.

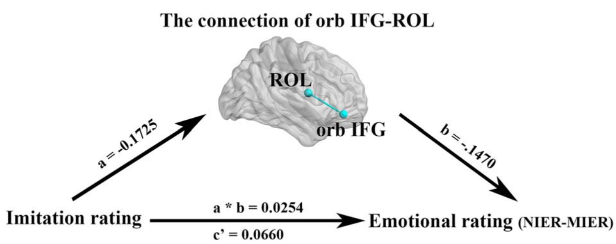


**Fig. 6.** The association between the imitation rating and the enhancement of IER effect was mediated by the functional connectivity of right orb IFG-ROL. Indirect path a = −0.1725; indirect path b = −0.1740; total relationship c = 0.0914; direct path c' = 0.0660; 95% bootstrap CI = [0.0012, 0.0803]; effect size = 27.79%.

effects and neural substrates of MIER on depressive intervention in clinical emotion dysregulation disorders.

## Author contributions

Jiazheng Wang (Experimental Design, Data collection, Data analysis, Writing—original draft), Jiemin Yang (Experimental Design, Writing—review & editing), Zhenzhen Yang (Data analysis), Wei Gao (Writing—review & editing), HeMing Zhang (Data analysis), Katherine Ji (Writing—review & editing), Benjamin Klugah-Brown (Writing—review & editing), JiaJin Yuan (Experimental Design, Project administration, Data analysis, Supervision, Writing—review & editing), and Bharat B. Biswal (Experimental Design, Project administration, Supervision, Writing—review & editing)

## CRediT author statement

Jiazheng Wang (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing—original draft, Writing—review & editing), Jiemin Yang (Conceptualization, Project administration, Supervision, Validation, Writing—review & editing), Zhenzhen Yang (Data curation, Formal analysis, Resources), Wei Gao (Conceptualization, Supervision, Writing—review & editing), HeMing Zhang (Formal analysis, Methodology), Katherine Ji (Writing—review & editing), Benjamin Klugah-Brown (Supervision, Writing—review & editing), JiaJin Yuan (Conceptualization, Funding acquisition, Project administration, Supervision, Validation, Writing—review & editing), and Bharat Biswal (Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Validation, Writing—review & editing)

## Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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## Data availability

The authors will supply the relevant data in response to reasonable requests.

## References

Amodio DM, Frith CD. Meeting of minds: the medial frontal cortex and social cognition. *Nat Rev Neurosci*. 2006:7(4): 268–277.

Bekkali S, Youssef GJ, Donaldson PH, Albein-Urios N, Hyde C, Enticott PG. Is the putative mirror neuron system associated with empathy? A systematic review and meta-analysis. *Neuropsychol Rev*. 2021:31(1):14–57.

Benedek Kurdi Lozano S, Banaji MR. Introducing the Open Affective Standardized Image Set (OASIS). *Behav Res Methods*. 2017;49(2):457–470. https://doi.org/10.3758/s13428-016-0715-3. PMID: 26907748.

Binder JR, Desai RH, Graves WW, Conant LL. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex*. 2009:19(12): 2767–2796.

Braadbaart L, de Grauw H, Perrett DI, Waiter GD, Williams JH. The shared neural basis of empathy and facial imitation accuracy. *NeuroImage*. 2014:84(1):367–375.

Buhle JT, Silvers JA, Wager TD, Lopez R, Onyemekwu C, Kober H, Weber J, Ochsner KN. Cognitive reappraisal of emotion: a meta-analysis of human neuroimaging studies. *Cereb Cortex*. 2014:24(11):2981–2990.

Butler EA. Temporal interpersonal emotion systems: the "TIES" that form relationships. *Personal Soc Psychol Rev*. 2011:15(4): 367–393.

Butler EA, Randall AK. Emotional coregulation in close relationships. *Emot Rev*. 2013:5(2):202–210.

Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, Lenzi GL. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc Natl Acad Sci U S A*. 2003:100(9): 5497–5502.

Carter RMK, Huettel SA. A nexus model of the temporal–parietal junction. *Trends Cogn Sci*. 2013:17(7):328–336.

Cavanna AE, Trimble MR. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain*. 2006:129(3): 564–583.

Chen S, Ding N, Wang F, Li Z, Qin S, Biswal BB, Yuan J. Functional decoupling of emotion coping network subsides automatic emotion regulation by implementation intention. *Neural Plast*. 2021:5: 6639739–6639712.

Cui F, Huang X, Jing Y, Luo YJ, Liu J, Gu R. How resource sharing resists scarcity: the role of cognitive empathy and its neurobiological mechanisms. *Cereb Cortex*. 2022:32(23):5330–5342.

Decety J, Jackson PL. The functional architecture of human empathy. *Behav Cogn Neurosci Rev*. 2004:3(2):71–100.

Dixon-Gordon KL, Bernecker SL, Christensen K. Recent innovations in the field of interpersonal emotion regulation. *Curr Opin Psychol*. 2015:3:36–42.

Friston KJ, Buechel C, Fink GR, Morris J, Rolls E, Dolan RJ. Psychophysiological and modulatory interactions in neuroimaging. *NeuroImage*. 1997:6(3):218–229.

Gao W, Biswal B, Chen S, Wu X, Yuan J. Functional coupling of the orbitofrontal cortex and the basolateral amygdala mediates the association between spontaneous reappraisal and emotional response. *NeuroImage*. 2021:232:117918.

Grecucci A, Theuninck A, Frederickson J, Job R. Mechanisms of social emotion regulation: from neuroscience to psychotherapy. In Bryant M. (ed). *Handbook on Emotion Regulation: Processes, Cognitive Effects and Social Consequences*. Haupauge, NY, USA: Nova Science Publishers, 2015; pp. 57–84.

Hofmann SG. Interpersonal emotion regulation model of mood and anxiety disorders. *Cogn Ther Res*. 2014:38(5):483–492.

Iacoboni M. Imitation, empathy, and mirror neurons. *Annu Rev Psychol*. 2009:60(1):653–670.

Inzlicht M, Gutsell JN, Legault L. Mimicry reduces racial prejudice. *J Exp Soc Psychol*. 2012:48(1):361–365.

Jabbi M, Swart M, Keysers C. Empathy for positive and negative emotions in the gustatory cortex. *NeuroImage*. 2007:34(4):1744–1753.

Jami PY, Walker DI, Mansouri B. Interaction of empathy and culture: a review. *Curr Psychol*. 2023;1–16. https://doi.org/10.1007/s12144-023-04422-6.

Kaplan JT, Iacoboni M. Getting a grip on other minds: mirror neurons, intention understanding, and cognitive empathy. *Soc Neurosci*. 2006:1(3–4):175–183.

Kim SH, Hamann S. Neural correlates of positive and negative emotion regulation. *J Cogn Neurosci*. 2007:19(5):776–798.

Lamm C, Silani G, Singer T. Distinct neural networks underlying empathy for pleasant and unpleasant touch. *Cortex*. 2015:70: 79–89.

Levy J, Goldstein A, Feldman R. The neural development of empathy is sensitive to caregiving and early trauma. *Nat Commun*. 2019:10(1):1905.

Li X, Meng X, Li H, Yang J, Yuan J. The impact of mood on empathy for pain: evidence from an EEG study. *Psychophysiology*. 2017:54(9): 1311–1322.

Marroquín B. Interpersonal emotion regulation as a mechanism of social support in depression. *Clin Psychol Rev*. 2011:31(8): 1276–1290.

McRae K, Hughes B, Chopra S, Gabrieli JD, Gross JJ, Ochsner KN. The neural bases of distraction and reappraisal. *J Cogn Neurosci*. 2010:22(2):248–262.

McRae K, Ciesielski B, Gross JJ. Unpacking cognitive reappraisal: goals, tactics, and outcomes. *Emotion*. 2012:12(2):250–255.

Menatti AR, Hopkins DeBoer LB, Weeks JW, Heimberg RG. Social anxiety and associations with eating psychopathology: Mediating effects of fears of evaluation. *Body Image*. 2015;14:20–28. ISSN 1740-1445. https://doi.org/10.1016/j.bodyim.2015.02.003.

Mobbs D, Yu R, Meyer M, Passamonti L, Seymour B, Calder AJ, Schweizer S, Frith CD, Dalgleish T. A key role for similarity in vicarious reward. *Science*. 2009:15(5929) 900:324.

Morelli SA, Lieberman MD, Zaki J. The emerging study of positive empathy. *Soc Personal Psychol Compass*. 2015:9(2):57–68.

Morris AS, Silk JS, Steinberg L, Myers SS, Robinson LR. The role of the family context in the development of emotion regulation. *Soc Dev*. 2007:16(2):361–388.

Mulej Bratec S, Xie X, Schmid G, Doll A, Schilbach L, Zimmer C, Wohlschläger A, Riedl V, Sorg C. Cognitive emotion regulation enhances aversive prediction error activity while reducing emotional responses. *NeuroImage*. 2015:123:138–148.

Murata A, Fadiga L, Fogassi L, Gallese V, Raos V, Rizzolatti G, Keysers C, Gazzola V, Ptrs B, Cattaneo L, et al. Object representation in the

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ventral premotor cortex (area F5) of the monkey. *J Neurophysiol*. 1997:78(4):2226–2230.

Ochsner KN, Silvers JA, Buhle JT. Functional imaging studies of emotion regulation: a synthetic review and evolving model of the cognitive control of emotion. *Ann N Y Acad Sci*. 2012:1251: E1–E24.

Onoda K, Okamoto Y, Nakashima KI, Nittono H, Ura M, Yamawaki S. Decreased ventral anterior cingulate cortex activity is associated with reduced social pain during emotional support. *Soc Neurosci*. 2009:4(5):443–454.

Reeck C, Ames DR, Ochsner KN. The social regulation of emotion: an integrative, cross-disciplinary model. *Trends Cogn Sci*. 2016:20(1): 47–63.

Riva F, Tschernegg M, Chiesa PA, Wagner IC, Kronbichler M, Lamm C, Silani G. Age-related differences in the neural correlates of empathy for pleasant and unpleasant touch in a female sample. *Neurobiol Aging*. 2018:65:7–17.

Sallquist J, Eisenberg N, Spinrad T, Wilkens N, Gaertner BM. Assessment of preschoolers' positive empathy: concurrent and longitudinal relations with positive emotion, social competence, and sympathy. *J Posit Psychol*. 2009:4(3):223–233.

Shamay-Tsoory SG, Aharon-Peretz J, Perry D. Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions[J]. *Brain*. 2009:132(3):617–627.

Sonnby-Borgström M. Automatic mimicry reactions as related to differences in emotional empathy. *Scand J Psychol*. 2002:43(5): 433–443.

Stel M, Blascovich J, McCall C, Mastop J, van Baaren RB, Vonk R. Mimicking disliked others: effects of a priori liking on the mimicry-liking link. *Eur J Soc Psychol*. 2009:40:867–880.

Wager TD, Davidson ML, Hughes BL, Lindquist MA, Ochsner KN. Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron*. 2008:59(6):1037–1050.

Walter H. Social cognitive neuroscience of empathy: concepts, circuits, and genes. *Emot Rev*. 2012:4(1):9–17.

Wang M, Zeng N, Zheng H, Du X, Potenza MN, Dong GH. Altered effective connectivity from the pregenual anterior cingulate cortex to the laterobasal amygdala mediates the relationship between internet gaming disorder and loneliness. *Psychol Med*. 2022;52(4):737–746. https://doi.org/10.1017/S0033291720002366. Epub 2020 Jul 20. PMID: 32684185.

Williams WC, Morelli SA, Ong DC, Zaki J. Interpersonal emotion regulation: Implications for affiliation, perceived support, relationships, and well-being. *J Pers Soc Psychol*. 2018;115(2): 224–254. https://doi.org/10.1037/pspi0000132. Epub 2018 May 7. PMID: 29733662.

Xie X, Mulej Bratec S, Schmid G, Meng C, Doll A, Wohlschläger A, Finke K, Förstl H, Zimmer C, Pekrun R, et al. How do you make me feel better? Social cognitive emotion regulation and the default mode network. *NeuroImage*. 2016:134:270–280.

Zaki J. Integrating empathy and interpersonal emotion regulation. *Annu Rev Psychol*. 2020:71(1):517–540.

Zaki J, Williams WC. Interpersonal emotion regulation. *Emotion*. 2013:13(5):803–810.

Zhang B, Liu J, Bao T, Wilson G, Park J, Zhao B, Kong J. Locations for noninvasive brain stimulation in treating depressive disorders: a combination of meta-analysis and resting-state functional connectivity analysis. *Aust N Z J Psychiatry*. 2020:54(6):582–590.

Zhao J, Mo L, Bi R, He Z, Chen Y, Xu F, Xie H, Zhang D. The VLPFC versus the DLPFC in down regulating social pain using reappraisal and distraction strategies. *J Neurosci*. 2021:41(6):1331–1339.

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