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Research paper

The neural mechanisms subserving the adaptiveness of emotion regulation flexibility and its link to depression

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ABSTRACT

Emotion Regulation Flexibility (ERF) is defined as an individual's ability to adaptively respond to changing situations and goals. Deficits in the adaptiveness of ERF have been linked to depression, suggesting a critical relationship between emotional processing and mental health. The objective of the present study was to investigate how variations in situational and goal-related contexts influence the association between ERF adaptiveness and depression. We employed functional magnetic resonance imaging (fMRI) and behavioral tasks to explore this relationship. Participants completed tasks designed to provoke changing situations and changing goals, while fMRI captured neural activity. Our findings revealed a significant negative correlation between depression scores and ERF adaptiveness. Specifically, during changing-situations, activation was observed in temporal and limbic regions, while changing-goals engaged prefrontal and parietal regions. Correlation analyses indicated that the adaptiveness of ERF was supported by distinct neural contributions: the temporoparietal junction (TPJ) in the changing-situations condition and the dorsolateral prefrontal cortex (dlPFC) in the changing-goals condition. Furthermore, the functional coupling between the dlPFC and the ventromedial prefrontal cortex (vmPFC) mediated the relationship between ERF adaptiveness and depression during changing-goals, but not during changing-situations. These findings elucidate the neural mechanisms of ERF adaptiveness and its implications for understanding and addressing depression.

1. Introduction

Inflexible emotional responses are typically maladaptive. This is because real-life situations and goals are constantly evolving. Emotion regulation flexibility (ERF) refers to an individual's capacity to adjust their emotional responses in real-time, based on the changing demands of situations and goals. The theory of ERF has proposed the adaptiveness of ERF to help us understand an individual's ability to respond flexibly, which is an important function of human survival and socialization development (Aldao et al., 2015; Gross, 2015). Adaptiveness of ERF refers to one's capacity to achieve different goals during emotion regulation and is believed to support individuals in adapting to complex living situations (Benita et al., 2021; Suri et al., 2017). While ERF is essential for adaptive emotional responses, its impairment is particularly pronounced in individuals with depression. In these individuals, both the ability to adapt to situations and pursue goals is often compromised (Joormann and Stanton, 2016; Nolen-Hoeksema, 2012). Deficits in ERF are particularly problematic for individuals with depression, as they struggle not only with maladaptive emotional responses but also with the failure to adapt to changing situations and pursue meaningful goals. Therefore, clarifying the neural mechanism underlying the adaptiveness of ERF has implications for our understanding of the development and maintenance of depressive symptoms.

However, until now little is known about the association between adaptiveness of ERF and maladaptive emotion regulation in depression. Previous research indicated that the adaptiveness of ERF is determined by two key factors: effectively coping with changing situations and successfully pursuing goals (Aldao et al., 2015; Millgram et al., 2020). In recent years, several studies have investigated the process of emotion regulation in changing situations. For instance, studies have shown that cognitive reappraisal—considered an adaptive emotion regulation strategy—may become ineffective in high-arousal situations, whereas

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expression suppression, typically viewed as maladaptive, may still offer short-term relief in high-stress situations (Silvers et al., 2015; Troy et al., 2013; Roos et al., 2018; Yuan et al., 2014). These findings highlight the complexity of emotion regulation strategies in depressive contexts. Prior clinical evidence supports the notion that emotion dysregulation contributes to the failure of goal pursuit in depression, which has been observed in multiple studies (Benita et al., 2021; Dickson et al., 2017; Jones et al., 2009). These failures are thought to be linked to both impaired emotional regulation and diminished motivation to achieve goals (Hajek and König, 2021; Wrosch et al., 2016). The cognitive control framework of ERF also suggested the influence of situational and goal-related factors on the emotion regulation process (Pruessner et al., 2020). It highlights how individuals monitor their emotional states, switch between various strategies, and suppress specific responses in order to adapt to changing situations and evolving goals within their environment. Taken together, it is crucial to uncover that the contribution of changing situations and goals to the adaptiveness of ERF.

While the link between ERF and depression has been explored in several studies, little is known about the neural mechanisms that support the adaptiveness of ERF, particularly in the context of changing situations and goals. This gap in knowledge limits our understanding of how ERF dysfunction contributes to the persistence of depressive symptoms. The adaptiveness of ERF is thought to be driven by two complementary neural mechanisms: bottom-up processes, which are triggered by situational stimuli, and top-down processes, which are guided by goals and expectations (Comte et al., 2016; de Kloet et al., 2019; Vanderhasselt and Ottaviani, 2022). These mechanisms help individuals respond appropriately to changing emotional demands. Previous studies found that the perception of situational stimulus has been attributed to bottom-up processing driven by emotional characteristics or evolutionary significance (Ochsner et al., 2009; Sussman et al., 2016). In other words, situational information not only allows us to perceive emotion but also guides us to make rapid adaptive responses, which is an essential aspect of the adaptiveness of ERF. Meanwhile, several studies showed that goal-directed behavior is primarily dominated by the top-down process (Buschman and Miller, 2014; Hwang et al., 2010). This process could improve emotional perception and regulation by guiding attention to different goals or changing resource allocation, which might be another way for ERF to benefit (Baluch and Itti, 2011; King et al., 2012). For instance, emotional face-related studies indicated that top-down goals guide the efficiency of facial expression search, and can improve emotional information detection (Brosch et al., 2010; Delchau et al., 2020). Additionally, research on mindfulness suggests that short-term emotion regulation effects are related to top-down processes, while long-term effects benefit from bottom-up processes, indicating that the adaptiveness of ERF may be influenced by both processes. (Chiesa et al., 2013; Zelazo and Lyons, 2012). Therefore, it is reasonable to explore the contribution of changing situations and goals to the adaptiveness of ERF from these two potential pathways.

Furthermore, cognitive neuroscience studies have demonstrated that there are dissociated bottom-up and top-down mechanisms within the cortico-limbic system during emotion regulation processes (Comte et al., 2016; Nicholson et al., 2017). An increasing number of studies suggested that individuals' emotional reactivity can be affected by situational stimulus, which has been associated with anterior cingulate, temporal, and subcortical regions involved in bottom-up processing. Specifically, prior research highlighted the role of anterior cingulate regions in monitoring internal emotional states, detecting emotional conflicts, and evaluating emotional salience, while the functional connectivity of the anterior cingulate cortex and amygdala modulate physiological response during automatic reaction processes (Etkin et al., 2010; Joormann et al., 2012). Moreover, other work indicated the function of the temporal lobe in situational information processing in emotional perception and episodic memory (Eichenbaum et al., 2012; Maratos et al., 2001), and by integrating emotional cues and situational information, it helps us to understand and respond to emotional stimuli, thereby shaping our emotional experience.

On the other hand, there is converging evidence suggesting that cognitive regulation of emotion involves the recruitment of a top-down network encompassing the dorsal and ventral prefrontal cortex, as well as the parietal cortex (Amit et al., 2015; Dörfel et al., 2014). The dynamic interplay between the prefrontal and parietal regions within the top-down network enables the implementation of goal-driven modulation of subcortical regions involved in emotion processing. For instance, several studies found that the strong inhibitory changes of connection strength between the inferior frontal gyrus (IFG) and dorsolateral prefrontal cortex (DLPFC) during goal-directed tasks aimed at regulating emotions effectively (Berboth and Morawetz, 2021; Morawetz et al., 2016), and individuals with disrupted frontal-parietal connectivity often experience difficulties in exerting cognitive control over their emotional responses (Nee, 2021; Wager et al., 2008). Collectively, the adaptiveness of ERF is likely to benefit from situations and goals through different neural pathways.

More importantly, current neurobiological models have emphasized the interactions between cortical and subcortical structures through multiple parallel bottom-up and top-down modulations in depression (Cristea et al., 2021; Vanderhasselt and Ottaviani, 2022). For example, brain imaging studies have found a dysfunctional activation recruitment of top-down prefrontal-subcortical circuitry, as well as impaired bottom-up connectivity from the amygdala to the subgenual anterior cingulate cortex in depression (Connolly et al., 2013; Park et al., 2019). However, little is known about how the dissociating bottom-up and top-down mechanisms underlie the adaptiveness of ERF in depression during changing situations and goals. Therefore, this study aims to address the research gap by testing two hypotheses: (1) that the anterior cingulate and temporal regions are involved in responding to changing situations, while the dorsal prefrontal and parietal regions are involved in goal adaptation, and (2) that the relationship between ERF adaptiveness and depression is mediated by the neural mechanisms of these changing situations and goals.

To investigate these hypotheses, we used functional magnetic resonance imaging (fMRI) alongside an individual-difference approach. This combination allowed us to measure both the neural response to situational and goal-related changes and the relationship between these neural activities and depressive symptoms. First, we detected the situation- and goal-related neural activities during the adaptiveness of ERF task. Subsequently, the correlation analyses and generalized psychophysiological interaction (gPPI) approach were conducted to probe the neural alteration driven by changing situations and goals. In addition, we also measured the levels of depression and the use of emotion regulation strategies in daily life, including reappraisal and suppression to examine the relationship between these measures and the adaptiveness of ERF scores. Finally, we explored the contributions of situation- and goal-related neural activities to the association between adaptiveness of ERF and depression by using mediation analyses.

2. Methods and materials

2.1. Participants

One hundred and ten right-handed, healthy participants (54 females) were recruited for the current study. The participants were aged 18 to 27 years ($M = 22.40$, $SD = 3.03$) and were recruited through university advertisements and were screened for health conditions prior to participation. Exclusion criteria included individuals with a history of psychiatric or neurological illnesses, substance use disorders, or severe medical conditions. This study was approved by the local ethical committee and the Institutional Human Participants Review Board of the Southwest University Imaging Center for human brain research. All participants gave written informed consent and were paid a nominal amount for their participation.

2.2. *Stimuli*

Picture stimuli consisted of negative and neutral pictures selected from the web, including 30 negative disgusts (e.g., vomit, feces), 30 negative fears (e.g., snakes, spiders), and 30 neutral pictures (e.g., wood, cars). All of the presented stimuli were pretested for arousal and valence in a preliminary experiment, negative disgust pictures ($M = 6.46$, $SD = 0.87$) and fear pictures ($M = 6.51$, $SD = 0.88$) were significantly more arousing than neutral pictures ($M = 4.02$, $SD = 0.69$, $ps < 0.001$); For valence ratings, negative disgust pictures ($M = 7.21$, $SD = 1.00$) and fear pictures ($M = 7.06$, $SD = 1.06$) led to significantly higher scores of valence than neutral pictures ($M = 4.19$, $SD = 0.62$). The stimuli were matched for luminance, complexity, and resolution to control for visual differences that might confound emotional responses. Picture stimuli (both negative pictures and neutral pictures) were also selected to match for size (15×10 cm^2) and resolution (100 pixels/inch), luminance and complexity.

2.3. *Behavioral assessment and experimental procedures*

On the same day of scanning, prior to the start of fMRI scanning, participants were first administered the Chinese version of the Emotion Regulation Questionnaire (ERQ). The ERQ was used to evaluate the dispositional use of emotion regulation strategies in daily life by measuring individual differences in suppression and reappraisal (Gross and John, 2003). Previous studies have used the ERQ to assess the association between the dispositional use of emotion regulation and depressive tendencies. The Beck Depression Inventory (BDI-II) (Beck et al., 1961) was used to assess the level of depressive risk in this study. The BDI-II consists of 21 items, and each item has a 4-point scale ranging from 0 to 3, assessing the severity of various cognitive, behavioral, and physiological symptoms associated with depression. The BDI-II can not only assess the intensity of depression but also detect possible depression in the general population, and it has a high validity and internal consistency (Wang and Gorenstein, 2013). In addition, measures of possible control variables include (i) the Chinese version of 48-item Neuroticism questionnaire of the Neuroticism-Extraversion-Openness Five-Factor Personality Inventory (McCrae and Costa Jr, 2004), which assesses individuals' preference to experience psychological distress; (ii) the State–Trait Anxiety Inventory (STAI) (Spielberger, 2010), which assesses individual differences in trait anxiety. Neuroticism and anxiety were measured as control variables because these factors are known to influence emotional regulation and depression. Specifically, high levels of neuroticism are associated with greater difficulty in regulating emotions, while anxiety can exacerbate emotional responses. By including these measures, we aim to control for their potential confounding effects in examining the adaptiveness of ERF.

We used an emotion regulation task adapted from Gao et al. (2024) to measure ERF. This task was specifically designed to assess how participants adaptively regulate emotions under different situational and goal conditions, allowing us to investigate both the cognitive and emotional aspects of ERF (Fig. 1A). In each trial, participants were first presented with a picture stimulus for 8 s, including different types of situational pictures. Participants were asked to react according to different goals at the top of the picture, including emotion regulation goals (□: regulation) and non-emotion regulation goals (△: memory). There were three experimental conditions (Fig. 1B): 1) congruent situations and goals in adjacent trials were identified as the conditions of no change (CNC); 2) congruent goals but incongruent situations in adjacent trials were identified as the conditions of situation change (CSC); 3) congruent situations but incongruent goals in adjacent trials were identified as the conditions of goal change (CGC). These conditions were chosen to evaluate how participants adapt to varying emotional regulation goals (e.g., emotion regulation vs. memory) and changing emotional stimuli. This approach enables us to assess the flexibility of emotional responses in dynamic contexts, thereby reflecting adaptive or maladaptive emotional regulation.

Following picture presentation, participants saw a jittered fixation

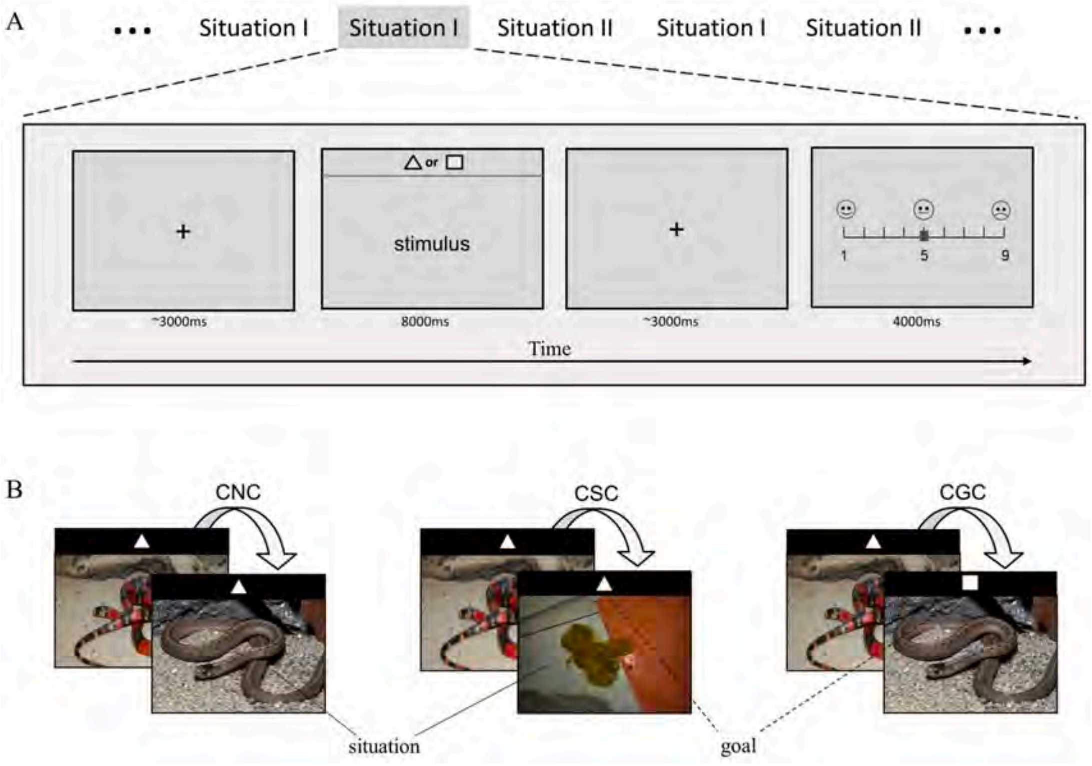

Fig. 1. A) The example trial sequence in the adaptiveness of ERF task; B) The experimental conditions in the adaptiveness of ERF task (CNC: the conditions of no change; CSC: the conditions of situation change; CGC: the conditions of goal change).

interval (jitter range = 2–5 s; mean duration = 3 s) and subsequently rated their affective state on a 9-point Self-Assessment Scale (SAM) (1 = Very good, 5 = No feelings, 9 = Very bad). After 30 min, participants need to finish a picture retrieval task by assessing their familiarity with pictures on a 9-point Scale (1 = Very unfamiliar, 5 = Uncertain, 9 = Very familiar), which was used to measure memory ratings to quantify the achievement of non-emotion regulation goals in two conditions. In this experiment, we recorded participants' actual performance as T scores including emotion rating and memory rating under different goals, which reflect the achievement of different goals for each condition, for more detail see the supplementary material. Following each run, participants were asked to assess their efforts to regulate emotions or remember pictures under different goals, recorded as *w* by using a percentage scale. Moreover, w*T assessed the level of adaptiveness for each goal, that is, individuals with higher w*T scores reflected better performance with personal goal-driven behavior. Finally, we used the formula: $Adaptiveness = \overline{\Sigma(w_1{*}\mathrm{T}_1 + \ldots + w_n{*}\mathrm{T}_n)}$ to calculate the overall performance of both emotion regulation and non-regulation goals, which assessed the achieved outcomes of different goal-driven behaviors in this experiment (Gao et al., 2024). The operation was consistent with the previous guidance, participants additionally practiced several trials on their own before taking part in the formal experiment.

2.4. FMRI data acquisition and preprocessing

Whole-brain fMRI data were acquired on the Siemens Trio MRI scanner of 3 Tesla (Siemens MAGNETOM Prisma 3T). Functional images were acquired with a T_2*- weighted, gradient-echo planner imaging (EPI) pulse sequence recording 33 sections oriented roughly parallel to the anterior and posterior commissure at an in-plane resolution of 3.4 × 3.4 × 3 mm^3 (TE = 30 ms; TR = 2000 ms; FA = 75°; FoV = 220 × 220 mm^2; 64 × 64 data acquisition matrix, 330 whole-brain volumes were recorded). Structural images were acquired with a T_1-weighted protocol (TR = 1900 ms, TE = 2.52 ms, FA = 9°, Matrix Size = 64 × 64, FOV = 256 × 256 mm^2, Voxel Size = 1 × 1 × 1 mm^3). Stimuli were presented using *E*-Prime and were projected onto a flat screen mounted in the scanner bore.

Preprocessing was performed using statistical parametric mapping (SPM12) tools (www.fil.ion.ucl.ac.uk) implemented in DPARSF (DPARSFA v5.3, http://rfmri.org/DPARSF) (Yan et al., 2016). Preprocessing comprised adjusting for variable acquisition time over slices (slice-timing), and head motion correction (realignment). Two steps were adopted in this study to control for the effects of head motion on the signals. First, if frame-wise displacement was found to be >0.5, then that time point was deemed a “bad” time point, and the time points before and after that bad time point were scrubbed using each of the bad time points as a regressor (Power et al., 2012). Second, only the subjects whose data satisfied our criteria for head motion, displacement of <3 mm in any plane and rotation of <3° in any direction were included in the final analysis. We performed these steps by using DPARSF and no participants were excluded because of motion artifacts according to our criteria. A total of 106 subjects were entered into the final data analysis. Then, normalization was conducted by applying DPARSF, which led to an improved registration between subjects. Normalization incorporated the following steps: (1) anatomical images of each subject were segmented using the “New Segment” procedure in SPM12; (2) the resulting gray and white matter images were used to derive a study-specific group template; (3) an affine transformation was applied to map the group template to the Montreal Neurological Institute (MNI) space; (4) subject-to template and template-to-MNI transformations were combined to create a single normalization transformation for each subject; (5) the normalization transformation for each subject was then applied to map. Finally, spatial smoothing using an 8 mm Gaussian kernel to increase signal-to-noise ratio.

2.5. Whole-brain analyses

Whole brain image analysis was completed with SPM12, and custom written programs in Matlab (R2017a, processing MathWorks, Inc., USA). Based on the general linear model in SPM12, we first analyzed individual data at the subject level. We were interested in the BOLD response of the brain to changing situations and goals; thus, the first level included three different conditions: CSC (changing situations), CGC (changing goals) and CNC (control condition), which to detect brain regions with altered activation during changing situations and goals compared to baseline. In addition, the design matrix also included six translational and rotational head movement parameters. These regressors were convolved with a canonical hemodynamic response function (HRF) and subjected to regression analysis for each voxel. This process allowed for the computation of the whole-brain response parameter (beta) maps during the three conditions. These parameter maps were used for group-level random-effect analysis, to locate any activation of changing situations and goals. To avoid possible false-positive results due to multiple comparisons, we adopted a peak-level correction to control the family-wise error rate (FWE) at $p < 0.05$ and a cluster threshold of $k > 20$ voxels. Subsequently, we conducted the whole brain correlation analyses (SPM12) to identify the brain regions in CSC and CGC that showed a significant correlation with adaptiveness of ERF scores on the group level.

2.6. Connectivity analyses

We performed a seed-to-voxel gPPI analysis based on brain regions that were significant in the whole-brain analyses analyses (regions showing significant cluster values change with adaptiveness of ERF scores). The steps of current analyses were consistent with several previous studies of functional connectivity (Murphy et al., 2016; Späti et al., 2015). The functional seed-to-voxel analysis was conducted with the CONN toolbox (v18; https://www.nitrc.org/projects/conn/) (Whitfield-Gabrieli and Nieto-Castanon, 2012). The CONN toolbox is suited for the analysis of functional connectivity in event-related designs, by conducting a generalized psycho-physiological interaction (gPPI) approach (see CONN manual v18; https://www.nitrc.org/projects/conn/) (Berger et al., 2017; Ginty et al., 2019). To correct for confounds of motion and physiological noise, the CONN toolbox implemented the anatomical component-based noise correction method (Behzadi et al., 2007), and extracting principal components related to the segmented cerebrospinal fluid (CSF) and white matter. This approach has been shown to increase the validity, sensitivity and specificity of functional connectivity analyses (Chai et al., 2012). Therefore, white matter and CSF noise components were used as confound regressors in the subject-level GLM. In addition, estimates of global signal and motion parameters were included as confound regressors. To control for simple condition-related activation effects, we also included the main task effects (CNC, CSC and CGC) as confound regressors in our functional connectivity analysis. Low-frequency drifts were removed via a high pass filter (128 s). The mean time-series were averaged across all voxels within each seed were used as a regression parameter, and correlated with all other voxels in the brain in a seed-to-voxel connectivity analysis. For the analysis, the CONN toolbox conducted a gPPI approach with connectivity measures calculated as bivariate correlations. This approach results in group-level statistics representing Fisher-z transformed correlation coefficient values.

2.7. Mediation analyses

To examine the contributions of situation- and goal-related neural activities to the association of emotion regulation adaptiveness and depression, mediation analysis was performed using the PROCESS macro (http://www. processmacro.org/) (Hayes, 2012). Mediation analysis was conducted to test whether neural activity in the identified regions mediates the relationship between ERF adaptiveness and depressive symptoms. This approach follows the logic of our hypotheses, which posits that the ability to adapt to changing situations and goals is crucial for effective emotion regulation. We expect that gPPI values, representing connectivity within key neural networks involved in emotion regulation, will provide insight into how variations in ERF relate to depressive symptoms. Mediation analysis calculates a bootstrap estimate of the indirect effect between the independent variable and dependent variable, an estimated standard error, and 95 % confidence intervals (CIs) for the population value of the indirect effect. The significance analysis was based on 5000 bootstrap realizations and the significance of indirect effects was assessed by applying a bootstrap method to the calculation of 95 % CI. Before conducting analyses, all variables were z-scored to produce standardized β weights. In this study, we extracted gPPI values for each ROI (regions showing significant cluster values change in the contrast of CSC > CNC and CGC > CNC) as mediating variables.

3. Results

3.1. Individual differences in behavioral measures

The distributions of the behavioral measures for depression in the present sample were as follows (18.35 ± 7.12) and adaptiveness (24.78 ± 2.72) with higher scores indicating greater emotion regulation adaptiveness. Pearson correlations revealed a significant negative association between the adaptiveness of ERF and depression scores ($r = -0.277$, $p = 0.004$) (Fig. 2A), indicating that individuals with higher ERF adaptiveness tend to experience lower depressive symptoms. The robustness of the bivariate association where then tested in regression using specified covariates (Fig. 2B). Hierarchical regression analysis, controlling for individual differences in emotion regulation strategies and personality characteristics, showed that ERF adaptiveness accounted for 22.4 % of the variance in depression scores ($p < 0.01$). This suggests a robust association between ERF and depression, independent of these factors. (More details see in supplement materials). These results indicated that the association between individuals' depressive risk and adaptiveness of ERF withstands the impact of other potential factors.

3.2. Neural patterns of changing situations and goals

Clusters of activation and deactivation for CSC and CGC versus CNC are shown in Fig. 3 and Table 1. There were clusters of significant activation in the contrast of CSC and CNC including the middle and inferior temporal gyrus, neighboring regions of the hippocampus and cuneus. Activation of the middle and inferior temporal gyrus, as well as the hippocampus, suggests that these regions are involved in processing emotionally salient stimuli, which is essential for adaptive emotional regulation. This activation indicates that the brain is effectively engaging in the evaluation of changing emotional contexts, which is critical for ERF. In contrast, deactivation in the anterior cingulate and middle frontal gyrus might reflect a reduction in emotional conflict processing when situations remain stable, suggesting a more efficient use of cognitive resources in stable contexts. Other areas of activation were seen in the cerebellum, extending occipital regions. Clusters of significant de-activation were seen in the middle frontal gyrus and the anterior cingulate areas. Deactivation in these areas could indicate reduced cognitive control or emotional regulation effort. This suggests a shift towards more automatic emotional processing in the absence of goal conflict, which is indicative of an adaptive response to stable emotional contexts.

The pattern of activations in the contrast of CGC and CNC showed more peak activities with the bilateral inferior parietal lobe and middle frontal regions, whereas clusters of significant de-activation were seen in the inferior frontal gyrus. These results indicated that changing situation- and goal-related neural activities were dominated by bottom-up (anterior cingulate and temporal regions) and top-down (prefrontal and parietal regions) processes, respectively.

3.3. Neural correlations in adaptiveness of ERF with changing situations and goals

To determine whether the effects of changing situations and goals could account for the adaptiveness of ERF, we further examined the associations of behavioral adaptiveness of ERF measures with the neural activities of CSC and CGC conditions. We calculated the correlations between adaptiveness of ERF scores and the modulation parameters in CSC and CGC conditions (Fig. 4). In the CSC condition, positive correlations between ERF adaptiveness and activity in the middle and

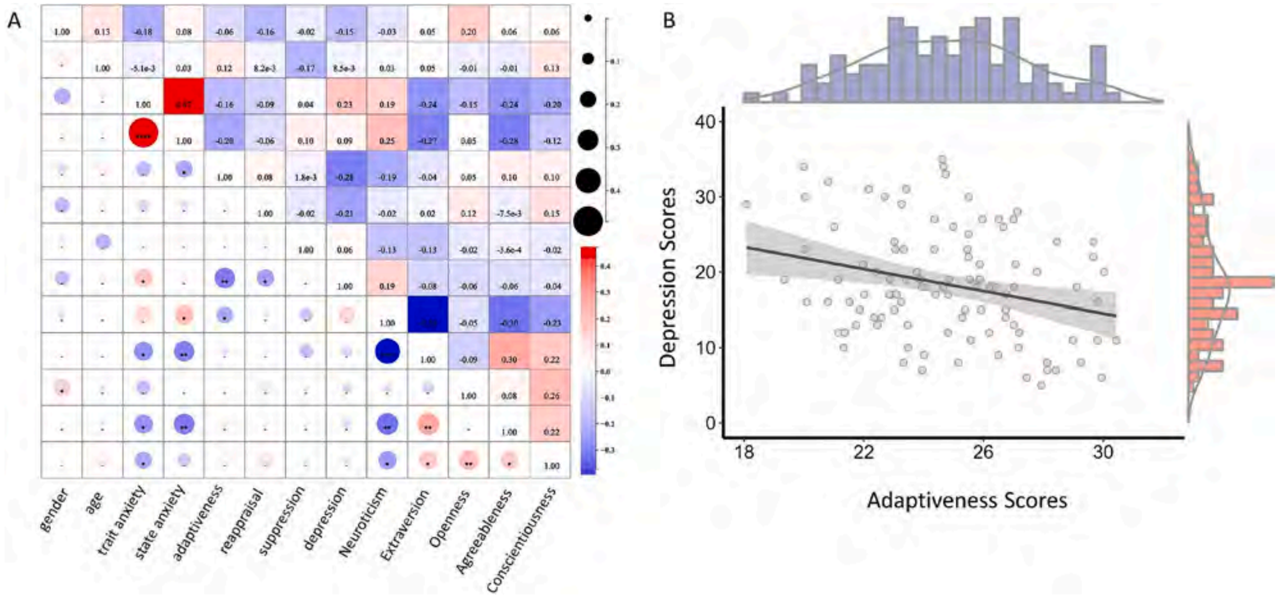

Fig. 2. A) Pearson correlation matrix of behavioral measurements and depression scores (*$p < 0.05$; **$p < 0.01$; ***$p < 0.005$). B) Significant OLS line showing a negative association between adaptiveness of ERF and depression scores after controlling for relevant covariates (OLS: ordinary least squares).

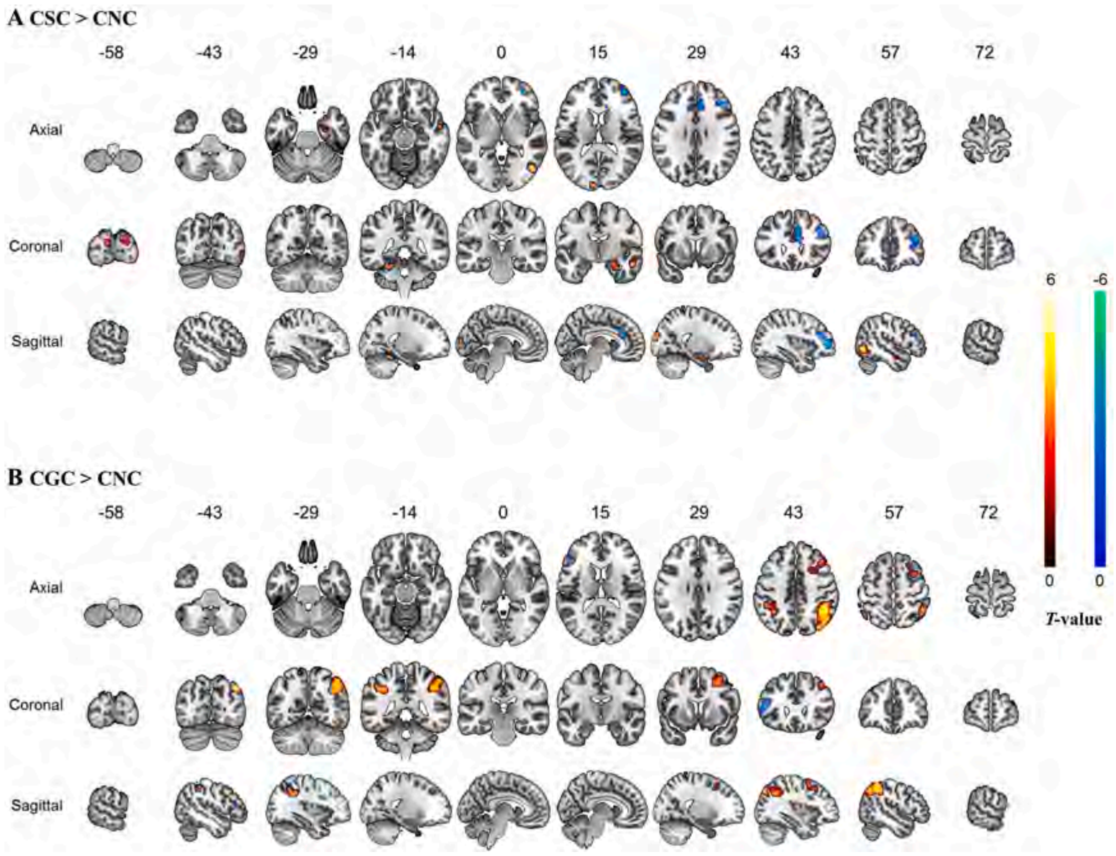

Fig. 3. Whole brain fMRI analyses examining activations and deactivations of the CSC > CNC contrast (A) and the CGC > CNC contrast (B).

Table 1
MNI coordinates of peak voxels and corresponding T that show significant activation and deactivation clusters ($k > 20$) when contrasting different experimental conditions in the whole sample.

Contrast	Brain regions	*H*	Peak coordinates (MNI)			*T*	*k*
			x	*y*	*z*		
CSC > CNC							
Positive activation	Middle Temporal Gyrus	R	54	−6	−18	5.66	34
	Inferior Temporal Gyrus	R	48	−69	−3	5.61	70
	Hippocampus	R	27	−12	−18	5.37	33
	Cerebellum	L	−21	−48	−21	5.01	40
	Cuneus	L	−9	−96	15	4.65	22
	Superior Occipital Gyrus	R	24	−90	21	4.58	23
Negative activation	Middle Frontal Gyrus	R	39	51	9	−6.21	150
	Anterior Cingulate	R	9	27	21	−4.92	67
CGC > CNC							
Positive activation	Inferior Parietal Lobule	R	42	−51	45	5.80	483
		L	−45	−42	42	4.33	85
	Middle Frontal Gyrus	R	27	9	51	4.02	132
Negative activation	Inferior Frontal Gyrus	L	−51	27	12	−4.17	27

superior temporal gyrus suggest that effective emotional regulation may rely on the ability to process emotionally salient stimuli. This indicates that these regions are crucial for integrating emotional information, contributing to the flexibility needed for adaptive emotional responses. In the CGC condition, significant positive correlations with the postcentral gyrus and inferior frontal gyrus highlight that goal-directed processes related to ERF are linked to sensory and motor areas involved in emotional regulation and decision-making, suggesting a multi-faceted approach to emotional adaptability. Clusters of significantly negative correlation with adaptiveness of ERF scores were found in middle frontal gyrus, bilateral thalamus and anterior cingulate.

3.4. Functional coupling of the dorsal-ventral prefrontal cortex mediates the association between adaptiveness of ERF and depression scores

For connectivity analysis, we conducted a seed-to-voxel connectivity analysis by using the significantly correlated adaptiveness of ERF as masks. To explore the contributions of situation- and goal-related neural activities to the association between adaptiveness of ERF and depression. We reported these functional couplings and extracted gPPI values for each ROI (regions showing significant cluster value change in the contrast of CSC > CNC and CGC > CNC) as mediators. Then, mediation analysis was performed to test whether these functional couplings could mediate the relationship between the adaptiveness of ERF and depression, which was conducted using a bootstrapping method (MacKinnon et al., 2004). Models were tested using the SPSS macro-PROCESS, which calculates a bootstrap estimate of the indirect effect between the independent variable and dependent variable, an estimated standard error, and 95 % confidence intervals (CI) for the population value of the indirect effect. As illustrated in Fig. 5, our results showed that when the adaptiveness of ERF was examined as the predicting factor, the functional coupling from the left dlPFC to vmPFC (−0.1295, −0.0112) was a significant mediator in the relationship between adaptiveness of ERF and depression scores. However, we did not find significant indirect effects of other functional couplings on depression scores (For more

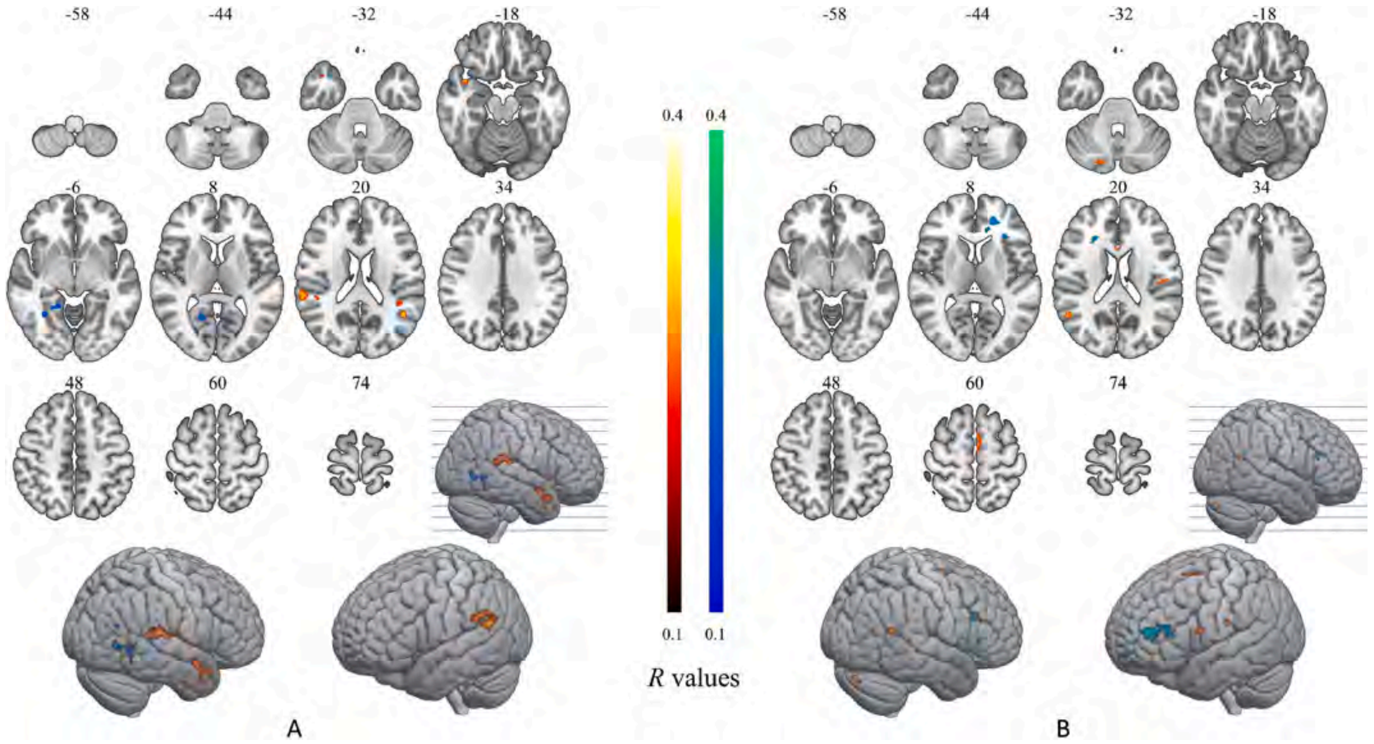

Fig. 4. A) Significant brain regions that adaptiveness of ERF scores correlated with changing situations; B) Significant brain regions that adaptiveness of ERF scores correlated with changing goals.

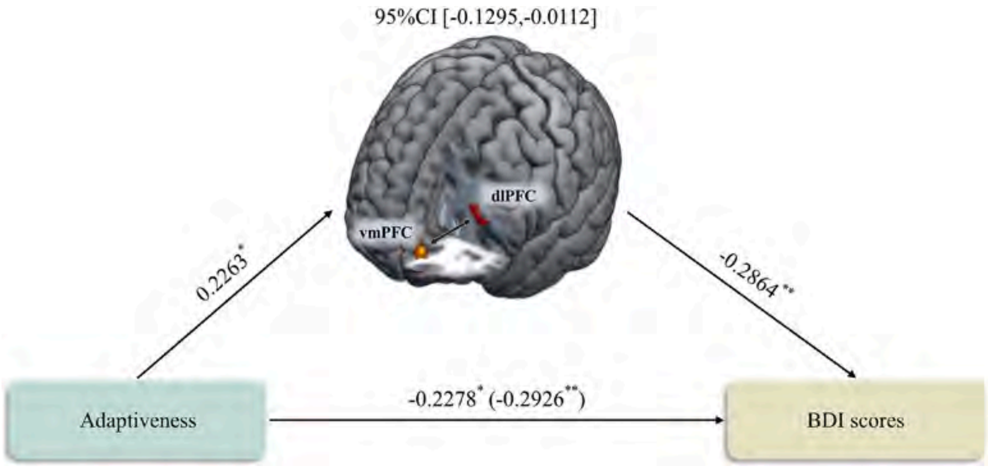

Fig. 5. The mediating effect of functional coupling of the left dlPFC-vmPFC on the association between adaptiveness of ERF and BDI scores. Indirect path a = 0.2263; indirect path b = −0.2864; total relationship c = −0.2926 and direct path c' = −0.2278. (**p* < 0.05; ***p* < 0.01; ****p* < 0.005).

details on mediation analysis, see supplementary material). A confidence interval (CI) that does not contain zero indicates that there is a significant mediation effect for the proposed mediating factor.

4. Discussion

This study explored how changing situations and goals impact ERF and its relationship with depression, utilizing fMRI to identify key neural systems involved. Our findings indicate that ERF adaptiveness is negatively correlated with depression levels, with situation- and goal-related neural activities primarily encompassing bottom-up processing in temporal and hippocampal regions, as well as top-down processing in prefrontal and parietal regions. Importantly, the functional coupling between the dlPFC and vmPFC mediated the relationship between ERF adaptiveness and depression. Together, these findings suggest goal-changing related emotion regulation processes are supported by neural activities in the prefrontal and parietal regions, especially the connectivity of the dorsal-ventral prefrontal cortex significantly contributes to the relationship between the adaptiveness of ERF and depression. The possible explanations, potential implications, and caveats of our findings are further considered below.

As expected, compared with the baseline condition, we found that changing situations elicited significant neural activities in the right inferior and middle temporal gyrus, as well as hippocampus areas. These activated brain regions have been reported in previous studies of contextual perception and episodic memory, which primarily serve the bottom-up stimulus-driven system (Nardo et al., 2011; Richter et al., 2019). The activation of the right inferior and middle temporal gyrus, in conjunction with the hippocampus, in response to changing situations supports the notion that bottom-up processes—driven by emotional salience—are crucial for the adaptive processing of emotional stimuli. These brain areas are well-established for their roles in the encoding and retrieval of emotional memories, assisting individuals in contextualizing and responding effectively to new emotional challenges (Eichenbaum et al., 2012; Mozaffari, 2014). For example, evidence of meta-analyses showed that the inferior temporal gyrus was associated with the processing of situational color, semantic information, and face-like objects, as well as the middle temporal gyrus has reliable activation during emotional perception with both face and scene stimulus types (Davey et al., 2016; Viard et al., 2012). On the other hand, prior studies have also highlighted the contribution of the hippocampus to the storage and extraction during self and episodic memory processing (Chadwick et al., 2010; Stella et al., 2012). Several recent studies found that the hippocampus is a crucial participant in the bidirectional interaction of memory and exploration processes that are iteratively engaged over binding together novel stimulus configurations to build episodic memories (Danieli et al., 2023; Reagh and Ranganath, 2023). Thus, it is possible that the role of the temporal cortex and hippocampus is to help individuals extract information about similarities from self-stored memories to identify the environment in which they are placed when the situation changes.

There are clusters with significant activation in the bilateral parietal lobule and right middle frontal gyrus during changing goals versus baseline condition. It has been demonstrated that areas most activated following top-down goals to attend to particular locations, features, or objects are located along the dorsal parts of the parietal cortex (Gazzaley and Nobre, 2012; Gottlieb, 2007; King et al., 2012). For instance, evidence from visual tasks has indicated that the inferior parietal lobe is preferentially activated when a stimulus of high goal-directed behavioral relevance (especially for unexpected cues), suggesting that this region is important for the interruption of current cognitive activity and the reorienting of attention (Fogassi et al., 2005; Sliwinska et al., 2015; Vickery and Jiang, 2009). Moreover, substantial research indicates that the middle frontal cortex is centrally involved in the pursuit of goals (Charron and Koechlin, 2010; Dixon and Dweck, 2022). Indeed, experimental evidence from executive function studies has revealed a multiple role for the middle frontal cortex, including the function of information monitoring and abstract rule processing, as well as instantiating motivational processes (Friedman and Robbins, 2022; Kouneiher et al., 2009). Here, one potential function for the middle frontal cortex is the integration of maintaining the motivational-goal processes and monitoring the behavioral-goal information. Together, neural activities in the parietal and middle frontal regions may serve for attentional reorientation and task rule selection with old and new goals, which are necessary for changing goals in the current study.

Moreover, the results of neural correlations indicated that different contributions of the temporoparietal junction (TPJ) and dorsolateral prefrontal cortex (dlPFC) to the adaptiveness of ERF. Several studies have documented that bottom-up attentional capture and orienting, mediated by stimulus salience, is subserved by the TPJ regions (Uncapher et al., 2011; Wu et al., 2015). For example, recent studies found that the TPJ is activated in response to potentially novel (unexpected or infrequent) stimuli or events when an organism is engaged in a neutral situation or when engaged in a task (Geng and Vossel, 2013; Igelström and Graziano, 2017). The positive correlation with TPJ activity suggests that individuals exhibiting high ERF adaptiveness are more adept at processing situational information and sensory stimuli, which is critical for flexible emotional regulation. This ability allows for a more nuanced response to varying emotional contexts, supporting adaptive emotional behavior. Conversely, the negative correlation with dlPFC activity indicates that those with high ERF adaptiveness might rely less on cognitive resources for emotion regulation, suggesting a more automatic or effortless regulation style (Brandl et al., 2019; Zaehringer et al., 2018). This automaticity in emotional processing could account for the observed decrease in emotional distress and lower susceptibility to depression among individuals with high ERF adaptiveness. Therefore, one reasonable explanation and speculation for our current results is that the adaptiveness of ERF benefits from the contributions of TPJ and dlPFC, which may be attributed to the function of effective emotion processing and effortless cognitive control, respectively.

Subsequent mediation analyses revealed the functional coupling of dlPFC-vmPFC plays a critical role in the association between adaptiveness of ERF and depression. In fact, the dlPFC has been implicated in top-down control functions and supported the integration and reprocessing of information during voluntary emotion regulation (Otto et al., 2014; Pozzi et al., 2021), while the vmPFC is involved in implicit emotion regulation because of its direct anatomical connection to subcortical regions, which are associated with the function of the bottom-up system (Park et al., 2019; Silvers and Moreira, 2019). Moreover, research on hierarchical cognitive control proposed the frontal lobes are a dynamic system with several different local networks that interact at a systems level to carry out complex tasks (Badre and Nee, 2018; Friedman and Robbins, 2022). Besides, altered dlPFC–vmPFC connectivity as one of the patterns identified in the meta-analysis, has been frequently observed in prior emotion dysregulation studies and thought to reflect abnormal communication between executive and default mode networks in depression (Connolly et al., 2017; Ng et al., 2019; Wilcox et al., 2016). The dlPFC plays a crucial role in top-down cognitive control and emotional regulation, allowing individuals to exert deliberate influence over their emotional responses. Conversely, the vmPFC is integral to implicit emotional processing and decision-making, helping individuals navigate emotional experiences based on contextual cues. This coupling between the dlPFC and vmPFC suggests that effective emotion regulation is facilitated by the integration of cognitive control mechanisms inherent in the dlPFC with the emotional processing capabilities of the vmPFC. This integrated functioning enables individuals to manage their emotional responses in a flexible and adaptive manner. Furthermore, disruption in this coupling, as observed in individuals with lower ERF adaptiveness, may lead to increased difficulties in regulating emotions, thereby contributing to the development and maintenance of depressive symptoms.

The following limitations need to be considered when interpreting these results. First, while this study provides important insights into the neural mechanisms underlying ERF, its ecological validity is limited by the controlled experimental tasks employed to assess ERF. These tasks may not fully represent the complexities of emotion regulation in real-world scenarios. Future studies could benefit from incorporating more naturalistic settings to better capture how individuals regulate their emotions in everyday situations. Second, although we controlled for preferences regarding specific emotion regulation strategies, it is important to acknowledge that strategy variability may influence ERF. The ability to flexibly switch between different regulation strategies depending on situational demands can be crucial for understanding ERF in daily life. Future research should investigate this variability and its effects on emotional responses. Third, we did not consider the effectiveness of a specific strategy in different situations because this study primarily focused on the general responses of individuals in coping with changing situations and goals. Given individuals' ability to select the appropriate strategy for different situations, we'll investigate the flexibility and adaptiveness of a specific strategy for a given situation in future work. Forth, this study included only behavioral measures and self-reported data, lacking more objective indicators. In future research, it is essential to collect physiological data (such as heart rate variability) as indicators of stress and emotional arousal during the tasks. Such measures would complement our behavioral and self-report data, providing a more comprehensive understanding of how adaptively participants managed their emotions under different conditions. Finally, since our sample consisted solely of healthy participants, the findings may not fully capture the complexities of ERF in clinical populations, particularly those individuals with depression. Future research should investigate whether the same neural mechanisms and functional coupling patterns observed in this study are present in clinically depressed individuals, as well as how these mechanisms may differ across various psychological conditions.

5. Conclusion

In the present study, we investigated the neural mechanisms underlying the adaptiveness of ERF, providing new insights into how changing situations and goals influence emotion regulation. Our results indicate that distinct neural patterns facilitate adaptability: temporal and limbic regions are essential for responding to situational changes by processing environmental information, while the prefrontal and parietal cortices support adaptability to changing goals through reorientation and executive functions. Importantly, our correlation analysis revealed that the adaptiveness of ERF is supported by contributions from the TPJ during the changing-situations condition and the dlPFC during the changing-goals condition, reflecting the roles of bottom-up and top-down processing, respectively. Furthermore, our mediation analysis demonstrated that the functional coupling between the dlPFC and vmPFC during the changing-goals condition mediates the relationship between ERF adaptiveness and depression. This coupling is crucial for maintaining emotional regulation and holds significant implications for preventing depression. These findings suggest that enhancing goal-driven adaptability may serve as a valuable target for interventions aimed at reducing the risk of depression. Future research should explore methods to strengthen the functional connectivity between the dlPFC and vmPFC to improve emotional regulation and prevent depressive symptoms in clinical populations.

CRediT authorship contribution statement

Wei Gao: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Bharat Biswal:** Writing – review & editing, Visualization, Resources, Methodology, Formal analysis. **Xinqin Zhou:** Writing – review & editing, Software, Methodology, Formal analysis. **Jintao Xing:** Visualization, Software, Methodology, Formal analysis. **Jiemin Yang:** Writing – review & editing, Supervision, Resources, Investigation. **JiaJin Yuan:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Formal analysis, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jad.2025.03.053.

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