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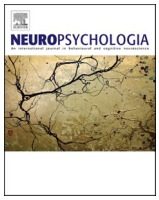

Amygdala-prefrontal connectivity during emotion regulation: A meta-analysis of psychophysiological interactions

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ABSTRACT

Given the importance of emotion regulation as a transdiagnostic factor in the development of psychopathology, a myriad of neuroimaging studies has investigated its neural underpinnings. However, single studies usually provide limited insight into the function of specific brain regions. Hence, to better understand the interaction between key regions involved in emotion generation and regulation, we performed a coordinate-based meta-analysis on functional magnetic resonance imaging (fMRI) studies that examined emotion regulation-modulated connectivity of the amygdala using psychophysiological interaction (PPI) analysis. We analyzed fifteen PPI studies using the activation likelihood estimation (ALE) algorithm. Investigating emotion regulation-modulated connectivity independent of regulation strategy and goal revealed convergent connectivity between the amygdala and the left ventrolateral prefrontal cortex (vlPFC), which was primarily driven by PPI studies implementing reappraisal as a regulation strategy. A more focused analysis testing for effective coupling during the down-regulation of emotions by using reappraisal specifically revealed convergent connectivity between the amygdala and the right dorsolateral prefrontal cortex (dlPFC), the left ventrolateral prefrontal cortex (vlPFC), and the dorsomedial prefrontal cortex (dmPFC). These prefrontal regions have been implicated in emotion regulatory processes such as working memory (dlPFC), language processes (vlPFC), and the attribution of mental states (dmPFC). Our findings suggest not only a dynamic modulation of connectivity between emotion generative and regulatory systems during the cognitive control of emotions, but also highlight the robustness of task-modulated prefrontal-amygdala coupling, thereby informing neurally-derived models of emotion regulation.

1. Introduction

Experiencing positive and negative emotions plays a central role in our daily life. The ability to regulate our emotions in a context-dependent manner by either up- or down-regulating emotional experiences is essential for our mental and physical health (Berking and Wupperman, 2012) as well as successful social interaction (Gross and John, 2003). In contrast, impairments in emotion regulation are associated with severe affective disorders such as depression and anxiety (Sloan et al., 2017). Thus, given that emotion regulation represents a transdiagnostic factor in the development of psychopathology, affective neuroscience has shown an intense interest in understanding the neural mechanisms that support the cognitive control of emotions during the last two decades. In particular, functional magnetic resonance imaging (fMRI) has been widely used to investigate the neuronal substrates of emotion regulation.

The most prominent framework for conceptualizing emotion regulation is the process model of emotion regulation that distinguishes five families of emotion regulation strategies (Gross, 1998): situation selection, situation modification, attentional deployment (via distraction: directing attention away from the emotional stimulus; or via concentration: focus on the emotional experience), cognitive change (via reappraisal: reinterpreting the emotional situation), and response modulation (via suppression: modifying the behavioral/physiological emotional response) (Webb et al., 2012). On a neural level, emotion regulation has been proposed to manifest on the interplay between multiple large-scale neural networks (Morawetz et al., 2020): Two cortical networks that are mainly implicated in the regulation of emotion, one subcortical network that is associated with emotion perception and generation and one that is linked to both, emotion regulatory processes and emotional reactivity. The cortical networks consist (i) of the dorsolateral prefrontal cortex (dlPFC), supplementary

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motor area (SMA), and inferior parietal cortex, which is related to working memory and response inhibition, and (ii) of the ventrolateral prefrontal cortex (vlPFC), SMA and temporo-parietal junction, which is mainly implicated in language processing. These cortical networks are supposed to act in a top-down manner to down-regulate the neural responses in subcortical regions such as the amygdala (e.g., Johnstone et al., 2007). The amygdala is part of the emotion generative network, that consists of the parahippocampal gyrus and ventromedial prefrontal cortex (vmPFC) and is supposed to act in a bottom-up fashion to detect and process emotional stimuli (McRae et al., 2012). Thus, it has been proposed that emotion generation precedes and might trigger emotion regulation implying an interaction between bottom-up and top-down processes (Dolcos et al., 2006; McRae et al., 2012). Indeed, previous findings found an interaction between emotion generation and regulation, which has been related to amygdala activation during reappraisal (McRae et al., 2012) and to coupling between the amygdala and the vlPFC during implicit emotion regulation (Dolcos et al., 2006) as well as coupling between the vmPFC and the amygdala during emotion generation and emotion regulation using distraction (Denkova et al., 2015).

This idea of interacting emotion-generative and regulatory networks (Barrett and Satpute, 2013; Morawetz et al., 2020; Ochsner et al., 2012) has mainly been investigated by fMRI studies using standard correlational analyses, examining the association between prefrontal control regions (e.g., the dlPFC) and subcortical emotion generative regions (e.g., the amygdala). However, the correlation of activity between different regions does not necessarily mean a change in connectivity between those regions during the task (Friston, 2011). One way to overcome this limitation is to directly test the effective coupling between regions by using Psychophysiological interaction (PPI) analysis (Friston et al., 1997). PPI is used to examine the interaction between a physiological (different brain regions) and a psychological variable (task conditions such as an emotion regulation condition and a control condition). By conducting voxel-wise analysis, regions, that show experimentally mediated changes in connectivity with a seed region, can be identified. Importantly, based on PPI analyses no causal inferences can be made about inhibitory or excitatory effects between the amygdala and prefrontal regions.

Despite the growing number of fMRI studies in the field, few studies to date tested the amygdala-frontal interaction in terms of effective connectivity during emotion regulation. When taken separately, these individual imaging studies demonstrate inconsistent findings regarding patterns of connectivity as well as proposed directions in connectivity changes. For example, Kanske et al. (2011) found enhanced negative connectivity between the left amygdala and frontal regions including the superior frontal gyrus (SFG), orbital frontal cortex (OFC), and vmPFC as well as temporal and parietal regions. bib_Morawetz_et_al_2017Morawetz et al. (2017a,b) found a slightly different pattern of regions that showed enhanced negative coupling with the left amygdala during the down-regulation of emotions: vlPFC, temporal and parietal regions as well as the anterior cingulate cortex (ACC). In contrast, Banks et al. (2007) found enhanced positive coupling during emotion regulation of the left amygdala with the dlPFC, OFC, dorsomedial prefrontal cortex (dmPFC), subgenual ACC, and inferior parietal lobe.

The inconsistency of these findings might be due to methodological factors such as different task designs, imaging methods and analyses, which represent a source of heterogeneity across studies. However, the small sample sizes and the associated low statistical power of most fMRI studies are major limitations of the current literature. These variations between studies have made it very difficult to interpret the differences in connectivity patterns. Thus, an analysis of consistency and convergence of results across experiments is a crucial prerequisite for the development of neurally-informed models of emotion regulation (Yarkoni et al., 2010). So far, only one study performed a meta-analysis on fMRI studies using PPI that investigated the functional coupling of the amygdala during emotion processing in general (i.e. fear processing, face processing, and emotion regulation) (Di et al., 2017). In a subsequent analysis, Di et al. (2017) report the findings of a meta-analysis based on five emotion regulation studies using a rather liberal threshold to determine task-modulated connectivity changes related to the amygdala. They found that the amygdala demonstrated connectivity with the left vlPFC and the cingulate gyrus. Given the very small number of studies and the liberal threshold, the interpretation of these findings is limited.

In this study, we aimed to synthesize the previous literature on the interaction between emotion generative and emotion regulatory regions. We performed a literature search on PPI studies in the field of emotion regulation independent of the seed regions. This explorative research approach revealed that the amygdala was upon the most often used seed regions to investigate functional connectivity during emotion regulation. Given the low number of studies using other seed regions (e.g., the vlPFC), only studies using the amygdala as a seed were used for further analyses. Thus, we performed the first coordinate-based meta-analysis of effective connectivity between the amygdala and other brain regions mediated by an emotion regulation task (1) independent of regulation strategy (e.g., reappraisal, distraction), regulation goal (up- and down-regulation) and stimulus valence (positive and negative pictures) and (2) dependent on regulation strategy (i.e. reappraisal) and regulation goal (i.e. down-regulation). Using this approach, we overcome fundamental statistical and methodological constraints of individual studies and accelerate progress in elucidating the neural mechanisms that underlie emotion regulation. Based on previous findings, we hypothesized that the amygdala would be coupled with prefrontal regions such as the dlPFC, vlPFC, dmPFC, and vmPFC.

2. Methods

2.1. Literature search and selection criteria

Literature research was conducted using PubMed (www.pubmed.com) searching for combinations of keywords: “emotion regulation”, “affective regulation”, “reappraisal”, “fMRI”, “functional magnetic resonance imaging”, “functional MRI”, “effective connectivity”, “functional connectivity”, “PPI” and “psychophysiological interaction analysis”. The search was limited to the January 1, 2000 to the September 30, 2020. Additional studies were identified by previous reviews and meta-analyses resulting in 326 identified records in total (Fig. 1).

In the following, the term “experiment” refers to any single contrast analysis, while the term “study” refers to a scientific publication, usually reporting several contrasts, i.e. experiments (Eickhoff et al., 2020; Müller et al., 2018).

All articles were examined and included for the subsequent meta-analysis based on the following criteria:

(1) We only included data from studies on mentally healthy adults, while results of patients or specific sub-group effects (e.g., gender differences) were not included. Articles including patients were only selected if they reported results for a control group separately, and only the control group was included.
(2) Only whole-brain fMRI studies that reported coordinates for brain activation or deactivation in standard anatomical reference space (Talairach/Tournoux; Montreal Neurological Institute (MNI)) were considered. Coordinates originally published in Talairach space were converted to MNI space using the algorithm implemented in GingerALE 3.0.2 (Eickhoff et al., 2012).
(3) We only included studies that compared PPI effects (a) for an emotion regulation condition to a control condition [reappraisal/distraction > maintain/baseline] or (b) between emotion regulation conditions [i.e. reappraisal > distraction].
(4) Only studies on explicit emotion regulation were included, as it has been shown that the amygdala is differentially activated by implicit and explicit emotion processing (Habel et al., 2007). This

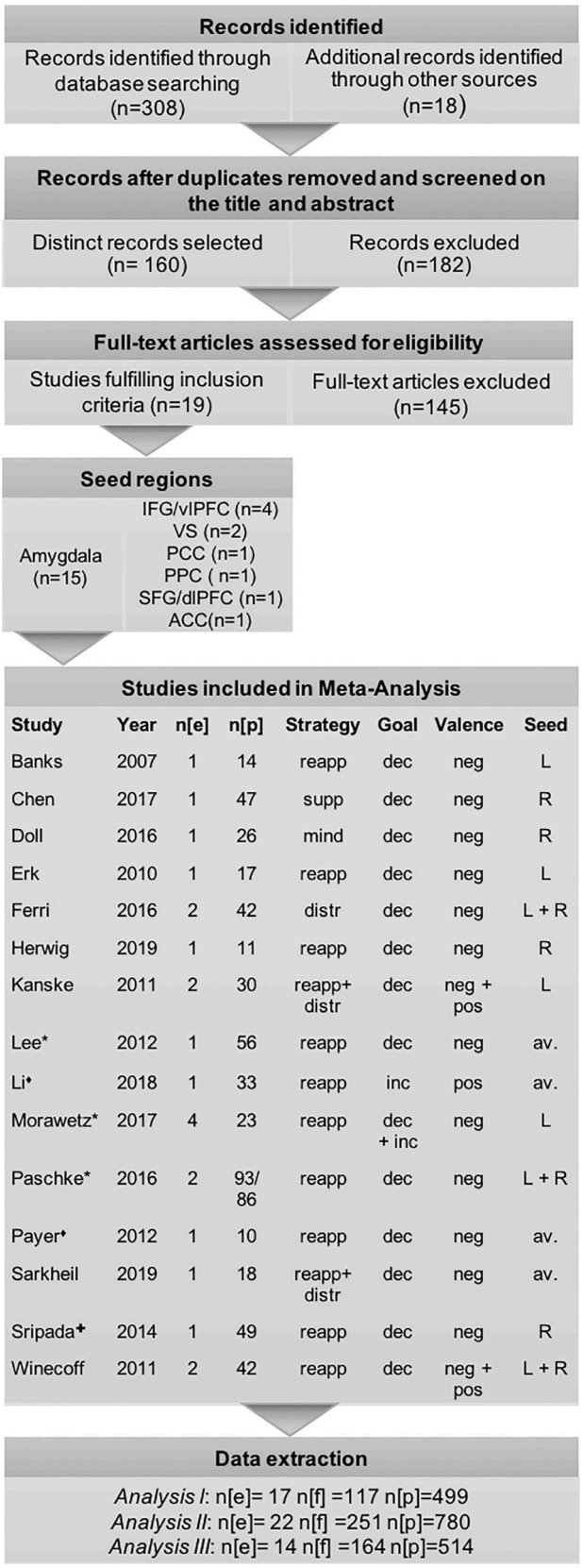

Fig. 1. Diagram outlining the study selection process. Studies included in the meta-analysis are described with regard to the investigated emotion regulation strategy, the regulation goal, the valence of the used stimuli and the seed region of the PPI analyses. *Analysis I* only included experiments without covariates. *Analysis II* included experiments with covariates. *Analysis III* only included experiments that used down-regulation via reappraisal.

means that a typical emotion regulation paradigm was used, in which participants are presented with a task that involves processing stimuli under two different conditions: A control condition, in which participants are asked to react naturally (maintain trial), and a regulation condition, in which participants are instructed to regulate their emotional responses (regulation trial). This inclusion criteria also ensured the generation of a relatively homogenous set of studies.

(5) Our literature search on PPI studies in the field of emotion regulation was performed independently of the seed regions. Upon the resulting studies that fulfilled inclusion criteria (1)–(4) (supplementary material, Table S1), the amygdala was the most often used seed region (15 studies), whereas other seed regions were only used in less than 5 studies (Fig. 1). Thus, we focused on examining amygdala-frontal coupling by only including studies using the amygdala as a seed region in the PPI analyses and reporting whole-brain analyses or results restricted to prefrontal cortex regions.

This search and the employed inclusion/exclusion criteria resulted in a total of 15 studies (780 participants) from peer-reviewed journals by September 30th, 2020 (Fig. 1). Most of the included studies (n = 10) implemented reappraisal as an emotion regulation strategy (Banks et al., 2007; Erk et al., 2010; Herwig et al., 2019; Lee et al., 2012; Li et al., 2018; Morawetz et al., 2017; Paschke et al., 2016; Payer et al., 2012; Sripada et al., 2014; Winecoff et al., 2011). Two studies implemented reappraisal and distraction via focusing on a concurrent task (Kanske et al., 2011; Sarkheil et al., 2019). One study used distraction via focusing on neutral aspects of the negative stimuli (Ferri et al., 2016). Two other studies used suppression (Chen et al., 2017) or mindfulness (Doll et al., 2016) to reduce negative affect, respectively. This imbalance between investigated regulation strategies reflects the current state of emotion regulation literature and has been determined previously in meta-analyses on emotion regulation (Morawetz et al., 2017a,b; Morawetz et al., 2020).

n: number of studies; IFG: inferior frontal gyrus; vlPFC: ventrolateral prefrontal cortex; VS: ventral striatum; PCC: posterior cingulate cortex; PPC: posterior parietal cortex; SFG: superior frontal gyrus; dlPFC: dorsolateral prefrontal cortex; ACC: anterior cingulate cortex; reapp: reappraisal; supp: suppression; distr: distraction; mind: mindfulness; dec: decrease; inc: increase; neg: negative; pos: positive; L: left amygdala seed; R: right amygdala seed, av.: left and right amygdala averaged as seeds, n[p]: number of participants – note, that the number of participants is added for every included experiment, hence participants are counted multiple times if more than one experiment of a study was included in the analysis; n[e]: number of experiments; n[f]: number of foci.

*Study included covariate in PPI analyses.

✚Study included covariate of no interest in first level PPI analyses.

◆Study used a prefrontal cortex mask.

2.2. Activation likelihood estimation (ALE) meta-analyses

Meta-analyses were performed using the revised version of the activation likelihood estimation (ALE) algorithm for coordinate-based quantitative meta-analyses of neuroimaging results as implemented in GingerALE 3.0.2 (Eickhoff et al., 2012). By combining the probabilities of all reported foci for each voxel in a given experiment, modeled activation maps (MA maps) were generated (Turkeltaub et al., 2012). The combination of all MA maps from all experiments was calculated to extract a voxel-wise ALE score that represented the convergence of results across experiments at each particular location in the brain. To distinguish 'true' convergence between studies from random convergence (i.e., noise), ALE scores were further compared to an empirical null-distribution, which represents a random spatial association between experiments (Eickhoff et al., 2012) and in which the same number

of activation foci was randomly relocated and restricted by a gray matter probability map (Evans et al., 1994). In line with recent guidelines based on massive ALE simulations (Eickhoff et al., 2016), ALE images were thresholded at a cluster-level corrected FWE threshold of $p_{cluster\text{-}level}<0.05$ (cluster-forming threshold at voxel-level $p_{voxel\text{-}level}<0.001$). Of note, due to the relatively small number of included studies, occasionally only one single study contributed to some resultant clusters. Therefore, we only report clusters that were contributed by at least two or more studies.

2.3. Individual meta-analyses

We performed three separate ALE analyses based on experiments investigating task-modulated connectivity with the amygdala as a seed region (Fig. 1). The first two analyses (*Analysis I* and *Analysis II*) included all studies on emotion regulation independent of regulation strategy and goal. *Analysis I* represents a restricted analysis, as it did not include any studies using covariates in the PPI analysis. In contrast, *Analysis II* extends *Analysis I* by including studies using covariates. Finally, to create a homogenous set of data, we performed a focused *Analysis III*, in which only studies using reappraisal to down-regulate emotions with or without covariates were included.

Analysis I. We conducted a restricted meta-analysis based on experiments reporting PPI main effects for emotion regulation independent of regulation goal and strategy and that excluded covariates. This analysis was based on 17 experiments, 117 foci, and 499 subjects. Note, that we only included one study using covariates of no interest in their first Level PPI analyses (e.g., current income (Sripada et al., 2014)).

Analysis II. We extended the previous analysis by including experiments that integrated individual difference factors as covariates in their PPI analyses such as e.g., emotion regulation success based on emotional state ratings (i.e., how successful participants are in regulating their emotions based on subjective emotional state ratings) (Morawetzet al., 2017) or based on electromyography (EMG) difference scores (i.e., trait-like emotion regulation ability measured by EMG activity over frowning muscles during regulation vs. a control condition) (Lee et al., 2012) or self-reported self-control (i.e., the ability to alter impulsive behavioral responses and thoughts to pursue overarching goals despite short-term temptations, which is associated with emotion regulation success) (Paschke et al., 2016). We included these studies, as they provide an insight into several factors that may moderate emotion regulation-modulated amygdala connectivity. Note, that this analysis was also independent of regulation goal and strategy. This analysis included 22 experiments, 251 foci, and 780 subjects. Studies using covariates are indicated with an * in Fig. 1.

Analysis III. Here, we aimed to perform a focused analysis in terms of regulation strategy and goal to create a homogeneous data set as other strategies and goals might induce variance. This means only studies using reappraisal as an emotion regulation strategy to down-regulate emotions were included as well as studies that fulfilled this criterion and used covariates. This analysis included 14 experiments, 164 foci, and 514 subjects.

3. Results

Analysis I did not result in any significant clusters.

The extended *Analysis II*, which included studies using covariates, revealed convergent connectivity with the amygdala during emotion regulation in the left IFG/vlPFC (Fig. 2A, Table 1). In total, 50% of the foci contributing to the vlPFC cluster used a covariate (emotion regulation success/self-control) in the PPI analysis. This demonstrates that the observed coupling between the vlPFC and the amygdala was not solely driven by studies implementing emotion regulation success/self-control as a covariate in the PPI analysis.

Analysis III, which tested for convergent connectivity during the down-regulation of emotions by reappraisal, revealed three regions

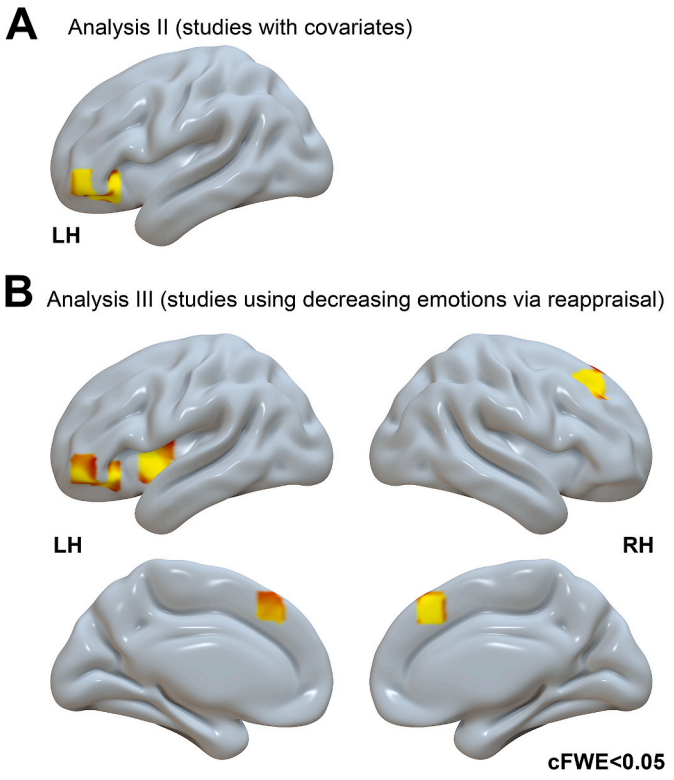

Fig. 2. Meta-analytic results of *Analysis II* and *Analysis III*. **A** *Analysis II* revealed convergent task-modulated coupling of the amygdala with the left inferior frontal gyrus (IFG)/ventrolateral prefrontal cortex (vlPFC) during emotion regulation compared to a control condition. **B** *Analysis III* – only including studies using reappraisal to down-regulate emotions – revealed convergent connectivity between the amygdala and three prefrontal regions: the left inferior frontal gyrus (IFG)/ventrolateral prefrontal cortex (vlPFC), the right superior frontal gyrus (SFG)/dorsolateral prefrontal cortex (dlPFC), and the medial frontal gyrus (medFG)/dorsomedial prefrontal cortex (dmPFC).

within the prefrontal cortex: (1) the left IFG/vlPFC, (2) the right SFG/dlPFC, and (3) the medial frontal gyrus (medFG)/dmPFC (Fig. 2B, Table 1). Of note, the same studies as in *Analysis II* contributed to the vlPFC cluster emphasizing the role of enhanced connectivity between the vlPFC and the amygdala during reappraisal in particular.

4. Discussion

In the current study, we aimed to examine structure-function relationships in the brain during the cognitive control of emotions. For this, we determined, which brain regions are effectively connected with the amygdala during regulatory processes by performing a coordinate-based meta-analysis on fifteen studies utilizing PPI. The extended meta-analysis *(Analysis II)* - including studies using a covariate *independent* of regulation strategy and goal - revealed convergent task-modulated coupling of the amygdala with the left vlPFC. The focused meta-analysis (*Analysis III)* – including studies using a covariate *dependent* of regulation strategy and goal – yielded increased connectivity between the amygdala and prefrontal cortex regions such as the dmPFC, the right dlPFC, and the left vlPFC. The more restricted meta-analysis *(Analysis I)* - only including studies reporting PPI main effects without a covariate, but *independent* of regulation strategy and goal - did not reveal any significant results, which might be due to the small number of experiments and participants (Eickhoff et al., 2016) and variance induced by the heterogeneity of the study designs.

Our results revealed that the left vlPFC is consistently coupled with the amygdala during emotion regulation, which means that this region might play a key role in the integration of information between emotion

Table 1
Studies contributing to the clusters resulting from *Analyses I-III*.

Analysis	Cluster	Volume (mm^3)	Coordinates			Study	Contrast	Goal	n[f]	Covariate	Amygdala seed
			x	y	z						
I	No sign. cluster										
II	left IFG/vlPFC	1016	−35	36	−9	Kanske et al. (2011)	reapp > distr	dec	1		left
						Morawetz et al. (2017)	reapp > control	dec	1		left
						Paschke et al. (2016)	reapp > control	dec	2	self-control	left
						Morawetz et al. (2017)	reapp > control	inc	1	regulatory success	left
						Sarkheil et al. (2019)	reapp > distr	dec	1		averaged
III	left IFG/vlPFC	912	−36	39	−8	Kanske et al. (2011)	reapp > distr	dec	1		left
						Morawetz et al. (2017)	reapp > control	dec	1		left
						Paschke et al. (2016)	reapp > control	dec	2	self-control	left
						Sarkheil et al. (2019)	reapp > distr	dec	1		averaged
	right SFG/dlPFC	672	24	28	43	Erk et al. (2010)	reapp > control	dec	1		left
						Paschke et al. (2016)	reapp > control	dec	2	self-control	left
						Paschke et al. (2016)	reapp > control	dec	2	self-control	right
	medFG/dmPFC	600	3	29	46	Sripada et al. (2014)	reapp > control	dec	1		right
						Paschke et al. (2016)	reapp > control	dec	1	self-control	left
						Paschke et al. (2016)	reapp > control	dec	1	self-control	right

Note. n[f]: number of foci, reapp: reappraisal; distr: distraction; control: control condition; dec: decrease; inc: increase. IFG: inferior frontal gyrus; vlPFC: ventrolateral prefrontal cortex; SFG: superior frontal gyrus; dlPFC: dorsolateral prefrontal cortex; medFG: medial frontal gyrus; dmPFC: dorsomedial prefrontal cortex.

regulatory and generative systems. Of note, all experiments contributing to the vlPFC cluster implemented reappraisal as an emotion regulation strategy. Thus, despite the strategy- and goal unspecific approach of *Analysis II*, convergent connectivity between the amygdala and vlPFC was mainly based upon reappraisal-related studies. This might be explained by the imbalance of the current literature as only a few studies to date implemented another regulation strategy apart from reappraisal using PPI. However, consistent activity within the vlPFC independent of regulation strategy or goal has been demonstrated in a meta-analysis (Morawetzet al., 2017). The left vlPFC has been implicated in language processes during emotion regulation and might support the active reinterpretation of the meaning of the emotional stimulus and facilitate the selection and implementation of goal appropriate reappraisals (Buhle et al., 2014; Kohn et al., 2014; Morawetz et al., 2020). This finding of convergent connectivity of the vlPFC with the amygdala replicates the results of Di et al. (2017) who also reported vlPFC-amygdala coupling during emotion regulation. In addition, the right dlPFC and dmPFC were consistently coupled with the amygdala during the down-regulation of emotional responses by reappraisal, specifically. The dmPFC is robustly recruited during tasks that require mental state inference and thus, supports attention to and evaluation of the mental states of the individuals depicted in these images in relation to the regulator's emotional state (Dixon et al., 2017). The dlPFC has been implicated in working memory and attention (Buhle et al., 2014; Kohn et al., 2014; Morawetz et al., 2020) and thus, activation of this region might be linked to the recruitment of greater cognitive resources during reappraisal (Rottschy et al., 2012; Silvers et al., 2015a,b).

The implication of the dorsal and ventral prefrontal network during reappraisal indicates an either direct or indirect (via other prefrontal regions) communication with the amygdala. Our findings suggest a direct functional link of the dlPFC and vlPFC as well as the dmPFC with the amygdala during the regulation of emotions. This is further corroborated by studies showing increased intrinsic resting-state functional connectivity between the vlPFC and the amygdala underlying successful emotion regulation (Morawetzet al., 2016) and increased negative functional connectivity during rest between the dmPFC and the amygdala (Roy et al., 2009), which is associated with lower levels of state anxiety (Kim et al., 2011). Additionally, anatomical studies showed dense reciprocal connections between prefrontal brain regions, e.g., the vlPFC and dmPFC, and the amygdala (Ghashghaei et al., 2007), while the more sparsely connected dlPFC regions possess greater input from than output to the amygdala (Ray and Zald, 2012). Thus, the dlPFC, playing a crucial role in successful emotion regulation (Kroes et al., 2019), might communicate with other prefrontal regions rather than directly interact with the amygdala. This is in line with a proposed feedback mechanism between dlPFC and vlPFC enabling the coordination of cognitive control processes and reappraisal (Morawetz et al., 2016a,b). Another widely discussed possibility is that cognitive control regions, e.g., vlPFC and dlPFC, act on the vmPFC, which is assumed to subsequently down-regulate the amygdala acting as an intermediate station (Urry et al., 2006). However, while some connectivity studies reported vmPFC-amygdala coupling during reappraisal (e.g., Silvers et al., 2017), meta-analyses failed to find evidence for vmPFC activation during cognitive reappraisal (Buhle et al., 2014; Morawetz et al., 2017). In our study, we also failed to find convergent connectivity of the vmPFC with the amygdala. One possible explanation is that the vmPFC, which plays a crucial role in evaluating the affective significance of stimuli and contexts (Silvers and Guassi Moreira, 2019), is engaged in naturally responding to an aversive stimulus as well as the explicit regulation of it (Buhle et al., 2014). Thus, due to the commonly used contrasts to investigate effective connectivity, i.e. a contrast between the regulation condition and a control condition, differences in vmPFC-amygdala connectivity might not be detectable. This idea has been supported recently by demonstrating vmPFC involvement in an emotion generative network (Morawetz et al., 2020).

Interestingly, the identified prefrontal regions were contributed by experiments using individual difference measures such as regulation success and self-control as covariates. Therefore, our results suggest that the strength of connectivity between the amygdala and the prefrontal regions might be additionally linked to and/or modulated by individual differences of reappraisal ability. This finding is confirmed by neurofeedback studies that specifically target the observed amygdala-frontal coupling to train emotion regulation ability. For example, Koush et al. (2017) observed an increase in effective top-down connectivity from the dmPFC onto the amygdala as a result of neurofeedback training. Moreover, emotion regulation training via neurofeedback of amygdala activation led to enhanced task-modulated connectivity of the amygdala with prefrontal regions including the vlPFC and dmPFC (e.g., Herwig et al., 2019).

In accordance with the previous literature that reported positive covariations between the amygdala and prefrontal regions during distraction (e.g., Denkova et al., 2015) and reappraisal (Urry et al., 2006; Wager et al., 2008), our study demonstrates an interaction between emotion generative and emotion regulatory processes in the case of effective connectivity between the amygdala and prefrontal regions. However, whether (a) the observed prefrontal regions dampen the activity in the amygdala (top-down) or (b) the activity in the amygdala induced by an emotional stimulus signals the prefrontal regions the need

for regulatory processes (bottom-up), remains unknown, as causality cannot be inferred from standard PPI analysis (O'Reilly et al., 2012). Future studies are needed to test the causal interaction between these emotion regulation key regions by implementing dynamic causal modeling.

4.1. Limitations

Several limitations should be noted. First, the interpretation of our meta-analytic results remains limited as the number of included studies is still rather small although we included three times more studies than Di et al. (2017) and used a sufficient corrected p-threshold to determine significant effects (Eickhoff et al., 2016). Second, given the limited number of studies, we were not able to differentiate between the up- and down-regulation of emotions, between different emotion regulation strategies as well as the reported direction of PPI effects (negative vs. positive). Thus, we cannot rule out that this combined analysis of different task designs might have biased our results of *Analysis I* and *Analysis II* to a certain degree, as in a previous study we found differential amygdala coupling with the PFC in response to the up- and down-regulation of emotions (Morawetzet al., 2017). Third, our study focused on explicit emotion regulatory processes only to increase the homogeneity of the dataset. However, this limits the scope of the present meta-analysis. Studies implementing implicit emotion regulation tasks such as e.g., emotional distraction (e.g., Dolcos et al., 2006), emotional conflict task (e.g., Chechko et al., 2013), affect labeling (e.g., Lieberman et al., 2007) or uninstructed emotion regulation (Silvers et al., 2015a,b), have been neglected and this issue needs to be addressed in future studies. Fourth, the included studies used either the left, right, or bilateral amygdalae as ROIs. Therefore, hemispheric differences within the amygdala, as indicated by previous literature (Baas et al., 2004; Sergerie et al., 2008; Wager et al., 2003), and their effects on connectivity patterns cannot be precluded. Fifth, it is commonly known that publication bias (meaning that the publication of studies depends on the direction and statistical significance of the results) represents a substantial problem for the validity of meta-analyses in particular (Jennings and Van Horn, 2012; Thornton and Lee, 2000; Van Aert, Wicherts and Van Assen, 2019). Especially in fMRI research, where the published results are primarily small-study effects, publication bias leads to the overestimation of these effects and thus, results in false impressions about the magnitude and existence of an effect. To overcome this issue, future studies could include results of unpublished research of registered studies or could base the meta-analysis on raw data of studies using PPI during emotion regulation. Finally, our meta-analyses focused only on the amygdala as a seed region. It would be of high interest to investigate the convergent coupling of other seed regions in the future. Despite these limitations, our results provide a starting point for future studies investigating the connectivity between emotion regulatory and emotion generative networks.

5. Conclusion

In the light of the ongoing reproducibility crisis our results are of high relevance as the need for replications of findings constantly increases (Aarts et al., 2015; Stanley and Spence, 2014). Meta-analyses allow to draw conclusions across a larger body of studies and thus, overcome the limitations of small sample sizes (Button et al., 2013) and the associated low statistical power of individual fMRI studies (Yarkoni, 2009). With regard to this, our work serves the goal to confirm and synthesize previous results, thereby supporting the reliability of PPI findings in the context of emotion regulation. In sum, our study provides evidence for the consistent task-modulated coupling between the amygdala and prefrontal cortex regions (dlPFC, vlPFC, and dmPFC) which might increase with regulation success. Thus, our findings inform neurally-derived models of emotion regulation and represent another step toward a cumulative science of functional integration of data across emotion regulation studies. Future studies need to examine whether activity in and connectivity between these regions could be used as a biomarker in translational neuroscience.

Credit statement

Stella Berboth: Methodology; Validation; Formal analysis; Investigation; Data curation; Writing – original draft; Writing – review & editing; Visualization. Carmen Morawetz: Conceptualization; Methodology; Validation; Formal analysis; Investigation; Data curation; Writing – original draft; Writing – review & editing; Visualization; Supervision; Project management; Funding acquisition.

Disclosure statement

The authors declare that they have no conflict of interest.

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Availability of data and material

The datasets generated during and/or analyzed during the current study are available in the Open Science Framework repository, https://osf.io/mh8vg/?view_only=edf5309962d64b32ba47c1be10cf4918.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2021.107767.

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