



Neural correlates of reappraisal considering working memory capacity and cognitive flexibility

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Abstract

Cognitive reappraisal of emotion is strongly related to long-term mental health. Therefore, the exploration of underlying cognitive and neural mechanisms has become an essential focus of research. Considering that reappraisal and executive functions rely on a similar brain network, the question arises whether behavioral differences in executive functions modulate neural activity during reappraisal. Using functional neuroimaging, the present study aimed to analyze the role of working memory capacity (WMC) and cognitive flexibility in brain activity during down-regulation of negative emotions by reappraisal in $N=20$ healthy participants. Results suggest that WMC and cognitive flexibility were negatively correlated with prefrontal activity during reappraisal condition. Here, results also revealed a negative correlation between cognitive flexibility and amygdala activation. These findings provide first hints that (1) individuals with lower WMC and lower cognitive flexibility might need more higher-order cognitive neural resources in order to down-regulate negative emotions and (2) cognitive flexibility relates to emotional reactivity during reappraisal.

Keywords Cognitive reappraisal · Working memory capacity · Cognitive flexibility · Prefrontal cortex · Emotion regulation

Jenny K. Zaehring and Rosalux Falquez have equally contributed to this article.

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Introduction

Emotions are powerful drivers of our behavior. However, individuals do not just passively experience emotions, but have a variety of emotion regulation (ER) strategies at hand to control “*what kind of emotions they have, when they have them and how they experience and express these emotions*” (Gross 1999, p. 557). Difficulties with successfully applying these strategies are core symptoms of numerous mental disorders (Aldao and Nolen-Hoeksema 2012; Aldao et al. 2010; Barnow 2012; Barnow et al. 2013; Joormann and Vanderlind 2014).

One of the most widely studied ER strategy in the literature is cognitive reappraisal. It is a form of cognitive change by which individuals deliberate emotion-eliciting stimuli in a way that modulates the emotional response to these stimuli (Gross 2002; Gross and Thompson 2007; Ochsner et al. 2004). Over the past decade, an increasing number of studies on the neural basis of reappraisal, including several meta-analyses, have been published (Banks et al. 2007; Buhle et al. 2014; Goldin et al. 2008; Kim and Hamann 2007; McRae et al. 2010; Morawetz et al. 2016). These studies demonstrate the involvement of higher-order cognitive areas in the lateral prefrontal cortex such as the ventrolateral

prefrontal cortex, dorsolateral prefrontal cortex, and middle frontal gyrus, which are important components of the executive frontoparietal network (Menon 2011) and are referred to as indispensable for the down-regulation of emotions via projections to the limbic system, in particular the amygdala (McRae et al. 2010; Okon-Singer et al. 2015; Urry et al. 2006).

Anatomically, the structures of the involved reappraisal network can be categorized according to their phylogenetic development (Ray and Zald 2012). Phylogenetically older regions such as the ventromedial prefrontal cortex, the orbitofrontal cortex, and the anterior cingulate cortex, including the subgenual anterior cingulate cortex, are directly coupled to the amygdala, with the strength of this coupling being predictive of the successful down-regulation of emotions (Banks et al. 2007). Phylogenetically newer regions are more strongly involved with executive control functions and are located within lateral prefrontal cortex parts, such as the ventrolateral prefrontal cortex, the dorsolateral prefrontal cortex, and the middle frontal gyrus (Aron et al. 2003; D'Esposito et al. 2000; Ray and Zald 2012; Rottschy et al. 2012).

Executive control functions underlie self-regulatory mechanisms (Engle et al. 1999; Hofmann et al. 2012; Miyake et al. 2000; Zelazo and Cunningham 2007) and are defined as higher-order cognitive functions that dynamically modulate other cognitive sub-processes supporting goal directed behavior. These functions are commonly divided in three separate yet moderately correlated subcomponents: *Working memory (WM)*, *cognitive flexibility (shifting)* and *inhibition* (Miyake et al. 2000). Inhibition refers to the ability to inhibit predominant responses and cognitions (Miyake et al. 2000) and represents a central mechanism of emotion regulation (Joormann and Gotlib 2008, 2010). Previous studies have considered inhibition as an important component of cognitive flexibility (Diamond 2013; Monsell 2003). Evidence for the involvement of WM and cognitive flexibility in reappraisal of emotional information have been shown previously (Malooly et al. 2013; McRae et al. 2012; Schmeichel et al. 2008). Cognitive flexibility allows the shifts between implementation and maintenance of new reappraisals, while WM is related to the maintenance and monitoring stages by implementing new reappraisals (Kalisch 2009).

WM represents a resource-limited system that involves processes of simultaneous maintenance and manipulation of task-relevant information during the performance of a cognitive task (Baddeley 2000, 2007; Kane et al. 2007; Kane and Engle 2002). There are notable individual differences in WM capacity (WMC), i.e., in the amount of task-relevant information one can retrieve in the presence of distracting material (Kane et al. 2007). Several investigations have reported that emotional distractor cues impair WM performance to a higher degree than neutral

distractors, which also seems to alter brain activity of control brain regions (Dolcos et al. 2007; Krause-Utz et al. 2012; Schweizer and Dalgleish 2016). Regarding cognitive reappraisal, it has been demonstrated that individuals with high WMC are better at appraising negative emotional stimuli in an unemotional manner than low WMC individuals (Schmeichel et al. 2008). Furthermore, impairments in updating task-relevant information in WM have been associated with less use of reappraisal (Joormann and Gotlib 2008; Schmeichel and Tang 2014; Schmeichel et al. 2008).

One recent study investigated the effects of WM training with emotional stimuli on the neural correlates of reappraising negative cues (Schweizer et al. 2013), wherein participants showed a spatially extended activation of phylogenetically older prefrontal cortex structures, specifically the subgenual anterior cingulate cortex, in addition to an increased activation in the frontoparietal network. Moreover, training resulted in improved reappraisal ability. We infer from their findings an additional recruitment of phylogenetically older brain regions, playing the proposed “key role” in reappraisal, which might ultimately lead to a greater efficiency within the reappraisal network. In other words, results might be interpreted in terms of WM training with emotional stimuli increasing the coupling of newer with phylogenetically older regions, which would allow the effortless detection and down-regulation of negative emotional reactivity. No other types of executive functions were measured in the study by Schweizer et al. (2013). Hence, it remains unclear as to whether the relationship between brain activity during reappraisal and WM performance extends to cognitive flexibility.

Cognitive flexibility is defined as the ability to flexibly alternate between tasks, thoughts or mental sets in the face of changing contingencies (Lezak 1995; Miyake et al. 2000). This alternation is accompanied by a delay in the initiation of the new task, referred to as *switch costs* (Monsell 2003). This delay is a standard measure for cognitive flexibility, assessed in tasks requiring participants to change between different tasks across consecutive trials. The larger the delay, the poorer the cognitive flexibility performance. Malooly et al. (2013) examined the link between affective flexibility and reappraisal and found that greater flexibility (lower switch cost) predicted the effectiveness of reappraisal. Similarly, higher levels of cognitive flexibility have been associated with more successful reappraisals (McRae et al. 2012). So far, the importance of cognitive flexibility has been highlighted in clinical investigations regarding reappraisal and mental health related emotional control in everyday life (Garland et al. 2015; Genet et al. 2013; Malooly et al. 2013). Therefore, the current study aimed to explore not only the associations between WM and reappraisal activation patterns, but also the latter's link with cognitive flexibility.

Interestingly, studies on both WMC and cognitive flexibility have shown that higher capacity is generally associated with less prefrontal cortex activity during cognitive performance (Armbruster et al. 2012; Rypma et al. 2002; Rypma and D'Esposito 1999, 2000), suggesting that higher capacity enables more efficient processing. However, to the best of our knowledge, the question remains whether a higher capacity is also associated with less prefrontal cortex activity in phylogenetically newer regions during cognitive ER. Furthermore, the results of a newer training study demonstrated for the first time that even “non-emotional”, purely executive control training could induce changes in amygdala reactivity to negative stimuli by strengthening amygdala-prefrontal connectivity (Cohen et al. 2016). This finding highlights the complexity of cognitive-emotional interactions in the brain (Okon-Singer et al. 2015; Pessoa 2008, 2010) and leads to the assumption that behavioral measures of cognitive task performance might be associated with amygdala reactivity during the down-regulation of negative emotions during reappraisal.

In summary, it has been assumed that the ability to shift flexibly to a new interpretation is supposed to allow the implementation of reappraisals, whereas WM processes are needed for the active maintenance of these new reinterpretations (Hofmann et al. 2012; Kalisch 2009). Considering the functional and neural overlap of reappraisal and WMC and cognitive flexibility, individual differences in these executive functions may modulate brain activation in phylogenetically older and newer prefrontal cortex regions during reappraisal. There is increasing scientific interest in understanding such modulations, given that reappraisal is of high clinical relevance; it is a particularly effective ER strategy linked to advantageous outcomes in terms of mental well-being and social functioning (Gross 2002; Gross and John 2003; Webb et al. 2012), and is therefore seen as one of the most adaptive ways to regulate emotions.

The present study

The main purpose of the present study is to investigate whether poorer performance in two reappraisal-related executive functions are associated with activation in phylogenetic newer areas, while a better performance is associated with activation in phylogenetic older areas. Secondly, we provide preliminary evidence on whether individual differences in WMC are associated with differences in overall brain activity during reappraisal. We are further interested in whether this effect might extend to individual differences in cognitive flexibility. This seems necessary to us, as these two executive functions share considerable overlap and are thus rarely separable (Miyake et al. 2000).

We expect that (1) WMC and cognitive flexibility performance of participants correlate positively with reappraisal ability, (2) WMC and cognitive flexibility performance are (a) negatively correlated with brain activity in phylogenetically newer, lateral prefrontal regions, (i.e. ventrolateral prefrontal cortex, middle frontal gyrus and dorsolateral prefrontal cortex), but (b) positively correlated with brain activity in phylogenetically older prefrontal cortex regions (i.e. subgenual anterior cingulate cortex, orbitofrontal cortex and ventromedial prefrontal cortex). These hypotheses are based on the observation that higher WMC is associated with less overall prefrontal activity (Rypma et al. 2002; Rypma and D'Esposito 1999, 2000) but WM training might lead to spatially extended recruitment of structures during reappraisal (Schweizer et al. 2013), which are phylogenetically older structures, in accordance to Ray and Zald (2012). Furthermore, in order to investigate the contribution of WMC and cognitive flexibility for the effectivity of emotional modulation via cognitive reappraisal, 3) we expect to find a negative association between executive performance and amygdala activity during reappraisal.

To address these hypotheses, we assessed cognitive flexibility and WMC of healthy volunteers and recorded their blood-oxygen-level dependent (BOLD) activation using functional magnetic resonance imaging (fMRI) while they applied self-focused reappraisal during the presentation of negative pictures. We aimed to explore the correlations of WMC and cognitive flexibility performance with BOLD activity of whole-brain activation during reappraisal. Moreover, we correlated them with BOLD activity of selected a-priori defined regions-of-interest (ROIs) in the reappraisal conditions. An additional goal of our study was to explore whether the frequency at which participants engage in reappraisal and other forms of cognitive ER strategies would be associated with WMC and cognitive flexibility, as better executive function abilities may facilitate the use of certain cognitive ER strategies that are associated with higher cognitive functioning such as reappraisal (McRae et al. 2012) and planning (Behmer and Fournier 2014; Schwartz 2006; Spiegel et al. 2013). Moreover, we assessed psychopathological symptoms and emotional perception abilities in order to control potential confounds.

Methods and materials

Participants

Twenty-five healthy volunteers participated in this study. For the present analyses, two subjects had to be excluded due to metal artifacts and technical problems during measurement. Another subject had to be excluded due to reported ambidexterity. Two female subjects had to be excluded due

to neurological abnormalities. The final sample thus consisted of twenty participants (13 women; $Age = 39.65$, $SD = 11.71$, $age\ range = 21\text{--}59$ years). All participants were recruited through advertisements in newspapers from the general population. Some of them belonged to a control group of a previous clinical study (Falquez et al. 2014) and some of them were students. Participants were either reimbursed with money or course credit. They were invited to participate if they met the following criteria: (1) right-handedness, (2) MRI compatibility (no metal embedded in body, not pregnant, not claustrophobic), and (3) no history of neurological or psychiatric disorders.

Demographic and psychopathological assessment

Intellectual abilities were measured by using the German *Multiple Choice Vocabulary Test* (MWT-B; Lehl 1976). To measure depressive symptoms and psychopathological symptomatology, participants completed the German version of the *Beck Depression Inventory* (BDI-II; Kühner et al. 2007) and to the German version of the *Brief Symptom Inventory* (BSI; Franke and Derogatis 2000), respectively.

Assessment of emotional perception and regulation

To document potential associations with subjective emotional perception, we assessed self-reported emotion perception by using the *Scale of Experience of Emotions* (SEE; Behr and Becker 2004), a self-administered questionnaire that measures how individuals perceive and evaluate their own feelings. Additionally, in order to measure how frequently participants apply cognitive ER strategies, we administered the German adaptation of the *Cognitive Emotion Regulation Questionnaire* (CERQ; Garnefski et al. 2002; Loch et al. 2011), a 27-item questionnaire, comprising the following nine conceptually different subscales: *Self-blame*, *Other-blame*, *Acceptance*, *Planning*, *Positive Refocusing*, *Rumination*, *Positive Reappraisal*, *Putting into Perspective*, and *Catastrophizing*.

Executive functions assessment

Working Memory Capacity (WMC)

In order to measure WMC, participants completed the *Counting Span Task* (Case et al. 1982). For the task, participants were presented with a series of displays on a computer screen, each comprising a varying number of green circles (targets) and grey circles (distractors). They were instructed to count aloud the number of green circles on the current display. When the participant finished counting, the next display emerged. During the counting of circles in each display they were not allowed to recall previous numbers.

At the end of a series, a display with three question marks (“???”) emerged, which signaled participants to recall all memorized numbers of the series. The number of displays per series increased from two to eight. Each trial consisted of three series and participants had to give a correct answer in at least one series to be able to continue with the next trial.

The test ended when participants were not able to recall one of the three series per trial. Participants were then assigned a WMC score equal to the number of displays per trial (ranging from 2 to 8). Thus, if participants ended with trial 5, the span score was 4. For a graphical description of the procedure of the Counting Span Task see Fig. 1.

Cognitive flexibility (switch costs)

To measure cognitive flexibility performance, participants completed the Trail Making Test (TMT; Tombaugh 2004). The TMT is a paper–pencil test and consists of two parts. Part A (TMT-A) involves connecting 25 consecutive numbers with a pencil on a sheet of paper as quickly as possible. Part B (TMT-B) is similar to part A, but involves connecting consecutive alternating numbers and letters (i.e. 1-A-2-B...). The amount of time required to complete part A and B represents the scores on each part respectively. The difference between score B – A is a measure of *switch costs*. Thus, higher B – A scores reflect higher levels of switch costs and thus lower cognitive flexibility performance. For correlation analyses of the behavioral and functional imaging data, the switch costs scores were *z*-standardized, and then reversed in its polarity (i.e. cognitive flexibility) in order to equal

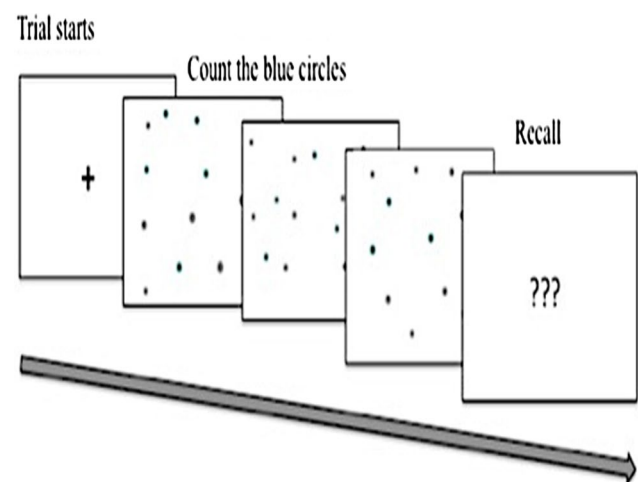


Fig. 1 Schematic of the Counting Span Task (Case et al. 1982). In each trial an increasing number of pictures were presented. Participants counted the blue circles for each picture and were required to store them in memory. At the end of the trial a screen with three question marks signaled the participants to recall the total numbers for each picture

the linearity of both variables. That means, + values were converted to – values, therefore higher values mean better cognitive flexibility performance, similar to WMC scores. Thus, we will refer to this “reversed” switch costs variable as “cognitive flexibility”, while the raw values will be called “switch costs”.

Reappraisal ability assessment

Stimulus material

For emotion induction during the reappraisal task, we selected a set of 20 negative and 20 neutral pictures from the *International Affective Picture System* (IAPS; Lang et al. 2005) already described in Falquez et al. (2014). The negative pictures were of unpleasant content showing mostly injured or mutilated people, violent situations and diseases. The neutral pictures showed mostly objects found in the home.

Reappraisal task

All participants were required to engage in a reappraisal task already used in Falquez et al. (2014). During reappraisal, participants were required to engage in *self-focused* reappraisal, i.e. to distance themselves from emotional stimuli by viewing the situation from a detached third-person perspective, thereby reducing its personal relevance. For example, one can reappraise a picture showing an injured person by imagining that this person has no personal connection to oneself. There were three experimental conditions: (1) *LookNew*: participants watched neutral pictures and were instructed to just naturally look at the screen. (2) *LookNeg*: Participants watched negative affective pictures and were also instructed to just naturally look at the screen. (3) *Decrease*: Participants watched negative affective pictures but now they were instructed to decrease the induced negative emotions by distancing themselves from the content of the pictures. The reappraisal task comprised 60 trials presented in a pseudo-randomized order using the

Presentation experiment driver (<http://www.neurobs.com>). At the beginning of each trial the participants looked at a white fixation cross on a black background for two seconds. Then, the instruction for each condition was presented for four seconds: Either “LOOK” or “DISTANCING”. After the fixation cross emerged again, either a negative or neutral picture was presented for six seconds. Participants had to process the pictures according to the previous instruction. Self-assessment Manikins (SAM Ratings; Bradley and Lang 1994) were presented directly after presentation of each picture. Participants had to rate on a 1–9 scale the amount of emotional arousal (1 = not arousing, 9 = highly arousing) and how displeasing the induced emotion (valence) was (1 = not displeasing, 9 = highly displeasing). Next, a random jitter (6–9 s) relax trial emerged on the screen. For a graphical description of the sequential procedure of the reappraisal task see Fig. 2.

Procedure

Participants attended two sessions that were no more than a week apart. In the first session, all participants completed an individual assessment that comprised demographic, executive and affective assessments. In the second session, participants completed the reappraisal task in the fMRI scanner. Before the reappraisal task, participants were handed a written instruction on how to complete the task. Then they were presented examples of negative pictures and were instructed on how to apply self-focused reappraisal. Three practice trials followed, where participants had to say out loud how they distanced themselves from the negative pictures. This assured that all participants applied self-focused reappraisal properly. The practice trial ended when the participant felt comfortable applying self-focused reappraisal. Then participants were laid in the MRI scanner and completed four additional practice trials to get familiar with the task and reappraisal procedure in the scanner. Finally, participants began with the actual task, consisting of two runs, each consisting of 30 trials.

Fig. 2 Schematic of the reappraisal task (modified from Ochsner et al. 2004). Each trial began with the instruction presented for 4 s. Then participants had to either look at or down-regulate the IAPS picture that emerged for 6 s according to the previous instruction. Afterwards, they rated emotional arousal and valence for 5 s each. Then participants relaxed (6–9 s) and the next trial started

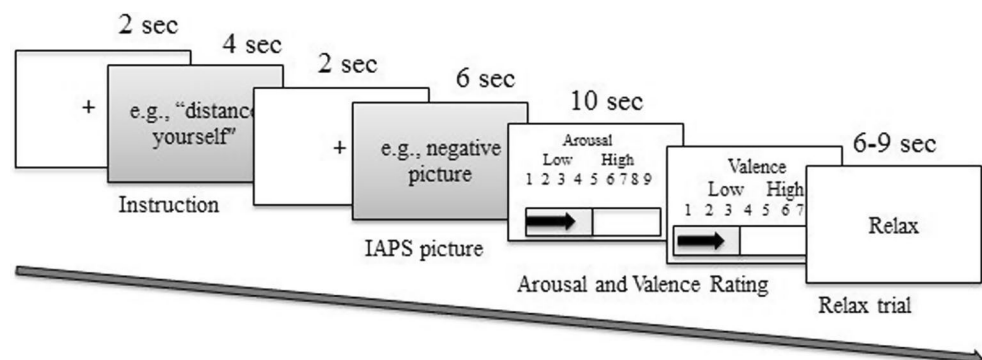


Image acquisition

BOLD images were recorded on a 3 T MRI scanner system (MAGNETOM Trio, Siemens Medical Systems, Erlangen, Germany) equipped with a 32-channel head coil at the University Hospital Heidelberg. Changes in BOLD T2-weighted MR signal were measured for each participant using a gradient echo-planar imaging sequence (repetition time [TR] = 2380 ms, echo time [TE] = 25 ms, 64×64 matrix, voxel size $3 \times 3 \times 3$ mm). Additional T1-weighted anatomical images (repetition time [TR] = 1680 ms; echo time [TE] = 2.6 ms; voxel size = $1.1 \times 1.1 \times 1.1$ mm) were measured for each participant to allow anatomical localization.

Data analysis

Behavioral data

Analyses of the behavioral data were performed using SPSS version 20 (SPSS Inc., Chicago, IL, USA). First of all, we ran repeated measure ANOVAs with arousal and valence ratings of LookNeu and LookNeg and of LookNeg and Decrease to make sure that participants were able to apply the reappraisal strategy (manipulation check). Additionally, following variables were computed: (1) Emotional reactivity was assessed by subtracting the arousal and valence ratings of the LookNeu condition from the LookNeg condition, and (2) Reappraisal ability was assessed by subtracting the arousal and valence ratings of the Decrease from the LookNeg condition. In order to further analyze the link between subjective emotional perception, ER strategy use, WMC and cognitive flexibility, correlations of WMC and cognitive flexibility with SEE and CERQ subscales were computed using Spearman's rho correlation coefficient with an assumed significance level of $p < .05$. We further correlated WMC and cognitive flexibility scores with emotional reactivity (LookNeg-LookNeu) and emotional regulation (Look Neg-Decrease) difference scores.

Functional imaging data

We analyzed the neuroimaging data using Statistical Parametric Mapping version 8 (Wellcome Department of Cognitive Neurology, London UK; <http://www.fil.ion.ucl.ac.uk/spm>). Pre-processing comprised adjusting for variable acquisition time over slices (slice-timing), head motion correction (realignment), normalization of images into a standard three dimensional space defined by the Montreal Neurological Institute (MNI), and spatial smoothing using an 8 mm Gaussian kernel to increase signal-to-noise ratio. In the first-level analysis, we defined the following regressors: LookNeu (presentation of neutral pictures, 6 s), LookNeg (presentation of negative pictures after the

instruction Look, 6 s). Decrease (presentation of negative pictures after the instruction Distancing, 6 s), and six movement regressors. In the second-level analysis, we looked at the neural activation at whole brain level for the following contrasts: LookNeu < LookNeg [emotional reactivity], and Decrease > LookNeg [reappraisal] –one-sample t-tests. Further, multiple regression analyses for each contrast were performed on a whole-brain level, with z-transformed WMC and cognitive flexibility scores as covariates. We used an exploratory probability height threshold of $p < .001$ (uncorrected). All coordinates are reported in Montreal Neurological Institute (MNI) format. In order to identify brain regions and their assigned Brodmann area (BA), we used the Wake Forest University (WFU) PickAtlas toolbox (<http://www.fmri.wfubmc.edu/download.htm>). For visualization of significant correlations at whole brain level, we extracted the mean parameter estimates averaged across 5 mm radius spherical masks of significant regions using the publically available MarsBar (<http://marsbar.sourceforge.net>), a toolbox implemented in SPM, and created scatter-plots showing significant associations.

In addition to the whole-brain analyses, we were especially interested in analyzing correlations between a priori ROIs of relevant phylogenetically older (subgenual anterior cingulate cortex, medial prefrontal cortex) and newer (ventrolateral prefrontal cortex, dorsolateral prefrontal cortex) regions in the prefrontal cortex with WMC and cognitive flexibility during reappraisal (cf., Poldrack 2007). For this purpose, we ran add-on ROI-analysis of circumscribed neural regions showing significantly changed activation patterns during reappraisal of negative stimuli after an emotional WM training according to Schweizer et al. (2013). We applied a multiple regression analysis in SPM with WMC and cognitive flexibility as covariates and anatomical masks of the following ROIs using the WFU PickAtlas toolbox: 1) phylogenetically older regions: (a) bilateral subgenual anterior cingulate cortex ($\pm 3/18/-9$) and (b) medial prefrontal cortex ($\pm 9/60/33$) and 2) phylogenetically newer regions: a) bilateral lateral prefrontal cortex (inferior: $\pm 57:60/15:24/3:15$; middle: $\pm 30/36/42$ and superior: $\pm 18/9/60$).

Results

Demographic and psychopathological measures

Participants had a mean IQ value of $M = 113.7$, $SD = 12.68$. Depression (BDI: $M = 2.2$, $SD = 2.8$) and psychopathological symptomatology (GSI: $M = 0.21$, $SD = 0.22$) scores were in the normal range. For demographic data of the whole group, see Table 1.

Table 1 Demographic data (N=20)

Variable		Mean	±	SD
Age		39.65		11.71
BDI-II		2.2		2.8
	GSI	0.21		0.22
BSI	PST	8.5		7.22
	PSDI	1.14		0.24
IQ		113.7		12.68

Note. BDI-II, Beck Depression Inventory II; BSI, Brief Symptom Inventory; GSI, Global severity index; PST, Positive symptoms total; PSDI, Positive symptoms distress index

Switch costs and WMC show normal kurtosis and skewness statistics, and arousal and valence ratings show acceptable kurtosis and skewness statistics. Thus, we can assume that assumptions of normal distribution were (see Table S1). For further correlation analysis, we reversed the z -standardized polarity of switch costs (i.e. cognitive flexibility) to ensure the same linearity as the WMC.

Manipulation check

We ran two repeated measure ANOVAs with arousal and valence ratings of the LookNeu and LookNeg and of the LookNeg and Decrease condition as within-subject factor. As shown in Fig. 3, mean valence and arousal ratings differed significantly across conditions. Mean arousal ratings were significantly higher in the LookNeg than in the LookNeu condition, $F(1,19)=305.39$, $p<.001$, partial $\eta^2=0.94$. Similarly, mean valence ratings were significantly higher in the LookNeg than in the LookNeu condition,

$F(1,19)=158.43$, $p<.001$, partial $\eta^2=0.89$. Likewise, mean arousal ratings were significantly lower in the Decrease than in the LookNeg condition, $F(1,19)=176.29$, $p<.001$, partial $\eta^2=0.90$. Mean valence ratings were significantly lower in the Decrease than in the LookNeg condition, $F(1,19)=158.45$, $p<.001$, partial $\eta^2=0.89$. Results demonstrate that the average valence and arousal ratings differed significantly between conditions, indicating that the induction of negative emotions was successful. Moreover, it should be noted that lower arousal and valence ratings reflect fewer negative emotions; therefore, we can assume that all participants were able to successfully apply reappraisal.

Behavioral data descriptives

WMC and cognitive flexibility did not correlate significantly with each other, $r=.20$, $p=.39$, which means that both variables might be independent from each other. WMC correlated significantly and positively with the CERQ subscales planning, $r=.63$, $p=.003$, and self-blame, $r=.56$, $p=.01$. All other correlations between WMC, cognitive flexibility, CERQ subscales, SEE subscales and SEE total score were not significant (for a detailed correlation matrix see Table S2 and S3) and therefore results on these correlations are not further discussed.

Reappraisal ability

Reappraisal ability did neither significantly correlate with WMC [arousal: $r=.19$, $p=.44$; valence: $r=-.04$, $p=.88$] nor with cognitive flexibility [arousal: $r=.15$, $p=.53$; valence: $r=-.18$, $p=.45$].

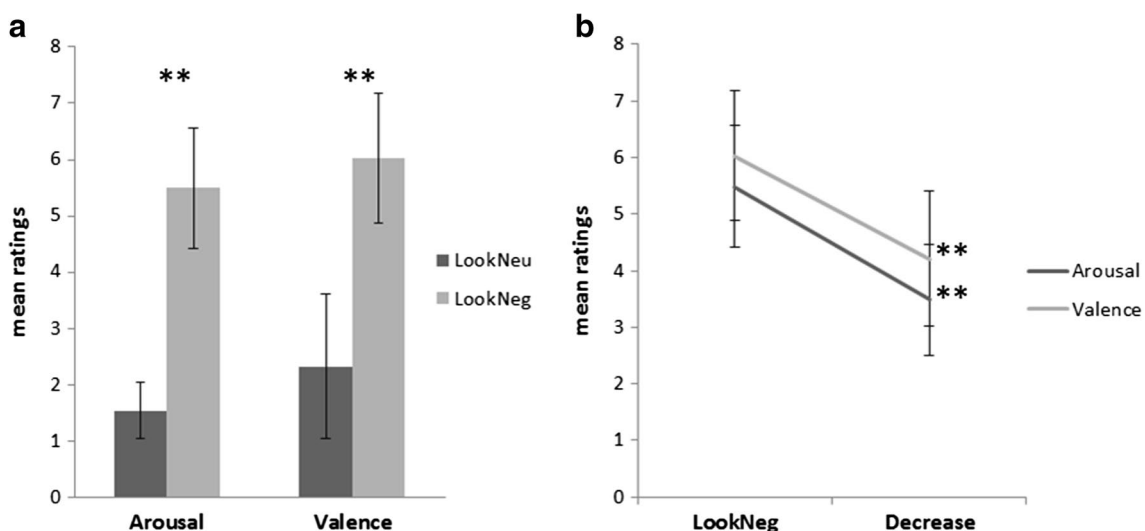


Fig. 3 Subjective mean ratings of arousal and valence (a) in the LookNeu compared to the LookNeg and (b) in the LookNeg compared to the Decrease condition (** $p<.01$). Error bars represent standard deviation ($N=20$)

Functional imaging data

Neural activity during emotional reactivity and reappraisal

On the whole-brain level, several cortical and subcortical regions were involved during the emotional reactivity condition (LookNeg > LookNeu; see Fig. 4a) including the right middle and superior temporal pole, bilateral amygdala and the left medial superior frontal gyrus. During the reappraisal condition (Decrease > LookNeg), regions of the bilateral inferior parietal gyrus, bilateral middle frontal gyrus, right superior frontal gyrus (BA8) were activated (see Fig. 4b). A hybrid illustration of uncorrected ($p < .001$) and corrected (FWE $p < .05$) brain activations for both contrasts are shown in Fig. 4 (cf., Bennett et al. 2009). For a complete list of activated brain regions during emotional reactivity and reappraisal see Table S4.

Multiple regression analysis

We examined how WMC and cognitive flexibility z -standardized scores, which were included in a multiple regression model as covariates, correlated with BOLD activity during

reappraisal (Decrease > LookNeg) across the entire brain. Results regarding correlations between emotional reactivity, cognitive flexibility and WMC were not focus of the present study but are reported in the supplement (s. Table S5 and S6).

WMC During reappraisal, WMC was negatively correlated with BOLD activity in phylogenetically newer regions such as the left middle frontal gyrus and the right middle cingulate region. WMC scores were not positively correlated with BOLD activity in any brain region (see Fig. 5a; Table 2). Results thus confirm hypothesis 2a), which states that WMC is negatively correlated with activation in phylogenetically newer prefrontal cortex regions, but contradict hypothesis 2b), which states that WMC is positively correlated with activation in phylogenetically older prefrontal cortex regions.

Cognitive Flexibility Similar to WMC scores, cognitive flexibility test scores were negatively correlated with phylogenetically newer regions such as the right inferior frontal gyrus (ventrolateral prefrontal cortex) and the right

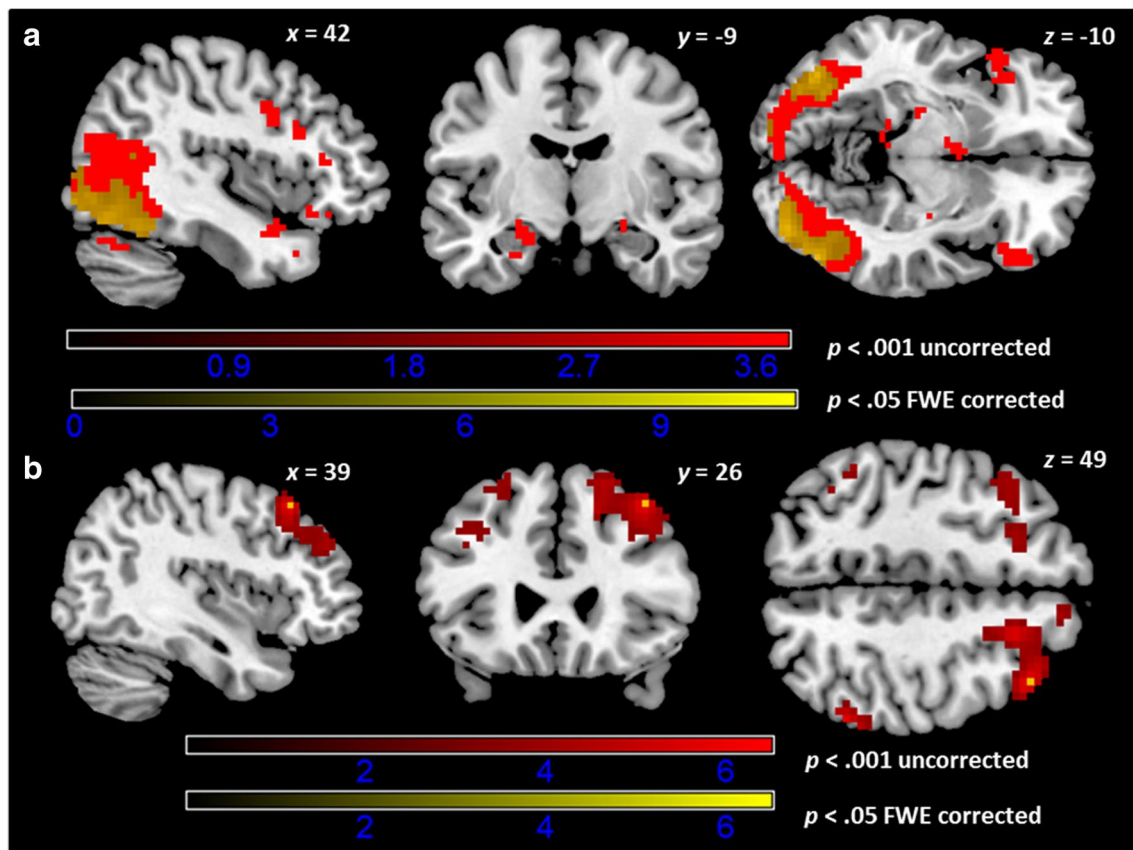


Fig. 4 Hybrid corrected/uncorrected presentation of activated brain regions during **a** emotional reactivity and **b** reappraisal conditions (at $p < .001$ uncorrected and $p < .05$ FWE corrected levels; $N = 20$)

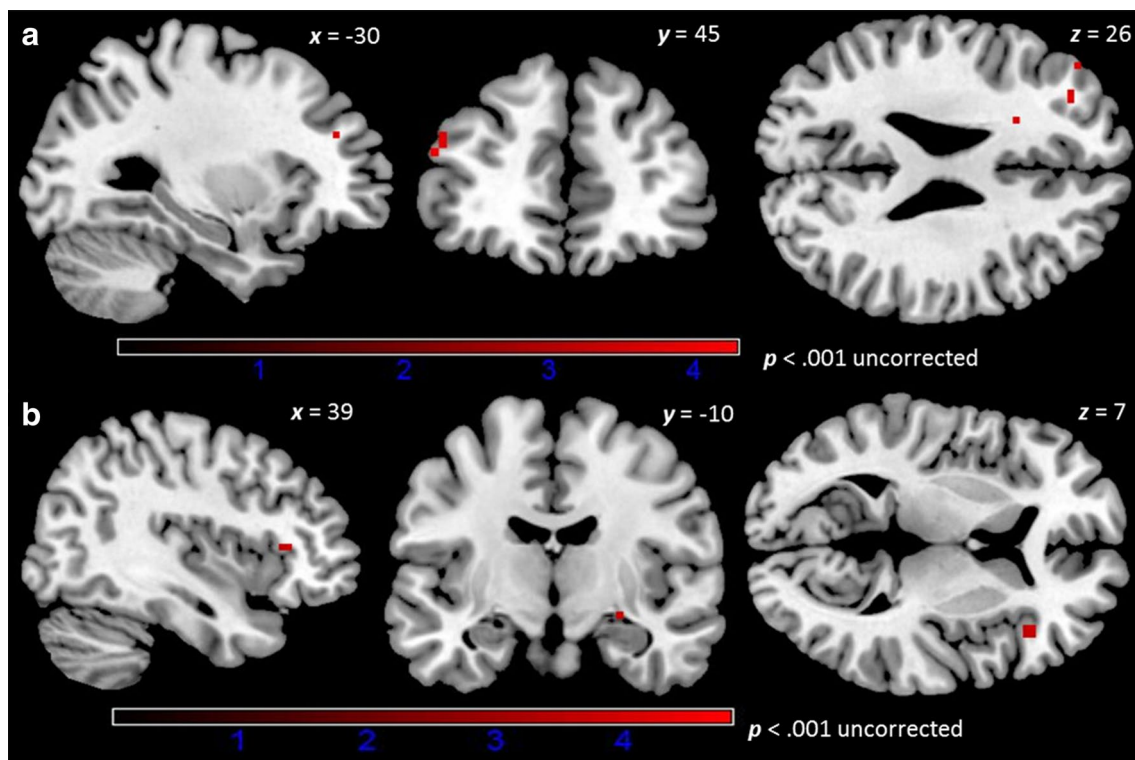


Fig. 5 Regions of correlation between brain activity during reappraisal and **a** working memory capacity and **b** cognitive flexibility performance ($p < .001$ uncorrected, $N = 20$)

Table 2 Regions of neural activation correlating positively (+) or negatively (-) with WMC in the reappraisal conditions ($N = 20$)

Brain Region	L/R	BA	k	MNI coordinates			T
				x	y	z	
<i>Decrease > LookNeg (-)</i>							
Middle Frontal Gyrus	L	46	4	-48	44	19	4.07*
	L	10	2	-30	41	25	3.84*
Middle Cingulate	R		2	15	-40	40	3.92

Note. Height threshold $p < .001$ uncorrected; MNI, Montreal Neurological Institute; k, cluster size in voxels; BA, Brodmann area; L, Left; R, Right, * $p < .001$ uncorrected, ROI-analysis

subgenual anterior cingulate cortex during the reappraisal condition, but were not positively correlated with BOLD activity in any brain region (see Fig. 5b). Interestingly, cognitive flexibility scores were negatively correlated with the amount of amygdala activation during the reappraisal condition, which might demonstrate that the higher the cognitive flexibility performance, the less amygdala activity during down-regulation of negative emotions.

For a complete list of activated regions see Table 3. Thus, the results demonstrated that during reappraisal participants with lower levels of cognitive flexibility showed higher BOLD activity in phylogenetically older and newer prefrontal cortex regions. Therefore, results again confirm hypothesis 2a) and contradict hypothesis 2b).

ROI-analysis results

The phylogenetically newer, prefrontal ROIs yielded significant results for the negative association between WMC scores and activation in regions in the left middle lateral prefrontal cortex during reappraisal, as shown in Fig. 6a. Furthermore, cognitive flexibility scores correlated significantly negatively with right ventrolateral prefrontal cortex (see Fig. 6b) in the same conditions. Regarding the phylogenetically older regions and limbic regions relevant for emotional processing, the right amygdala correlated significantly negatively with cognitive flexibility scores in the reappraisal condition ($p < .05$ FWE corrected; see Fig. 7).

However, ROI-analysis yielded no FWE corrected significant results regarding positive correlation of WMC and

Table 3 Regions of neural activation during reappraisal correlating positively (+) or negatively (-) with cognitive flexibility scores (N=20)

Brain Region	L/R	BA	k	MNI coordinates			T
				x	y	z	
<i>Decrease > LookNeg (-)</i>							
Cuneus	R		5	15	-70	-32	4.83
Cerebellum 6	L		15	-12	-67	-29	4.51
Inferior Frontal Gyrus	R		4	39	29	7	4.00*
Inferior Occipital Gyrus	L		2	-36	-67	-8	3.97
Amygdala	R		6	27	-4	-20	3.82**
Fusiform Gyrus	L		1	-42	-52	-14	3.80
	L		1	-39	-58	-11	3.66
Middle Temporal Gyrus	R	21	1	63	-43	-2	3.74
	R		1	57	8	-35	3.66
Olfactory Bulb	R		3	24	11	-14	3.71**
Vermis 3	R		1	3	-40	-8	3.66

Note. Voxel threshold $p < .001$ uncorrected; MNI, Montreal Neurological Institute; k, cluster size in voxels; BA, Brodmann area; L, Left; R, Right

* $p < .001$ uncorrected (ROI-analysis)

** $p < .05$ FWE corrected (ROI-analysis)

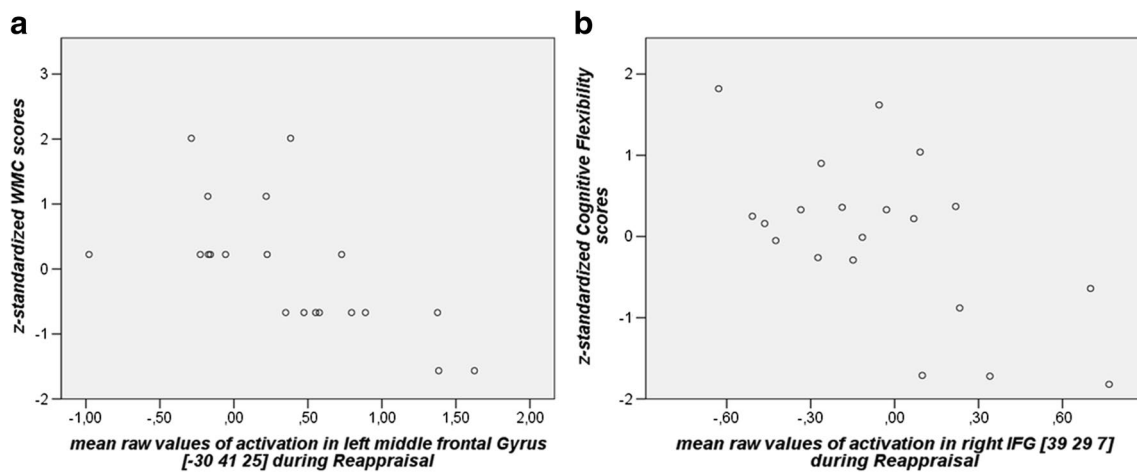


Fig. 6 Scatterplots showing a **a** negative association between WMC scores and activation in left lateral superior frontal gyrus during the reappraisal condition and **b** a negative association between cognitive flexibility and right IFG activation in the same condition (N=20)

cognitive flexibility with neural activation during reappraisal. On the other hand, a region near the subgenual anterior cingulate cortex (Olfactory Bulb) and right amygdala correlated significantly negatively with cognitive flexibility scores in the reappraisal condition. This finding defied our expectation of a positive correlation between cognitive flexibility performance and the involvement of older phylogenetic regions during reappraisal (Hypothesis 2b). Overall, cognitive flexibility scores might be negatively associated with the activation of both newer and older phylogenetic regions.

Discussion

The present study aimed to examine WMC and cognitive flexibility with respect to their association with the activity of phylogenetically newer and older brain regions during reappraisal. Moreover, it aimed to analyze whether WMC and cognitive flexibility are associated with reappraisal ability and the extent to which participants applied cognitive ER strategies in everyday life. We expected that WMC and cognitive flexibility performance of participants

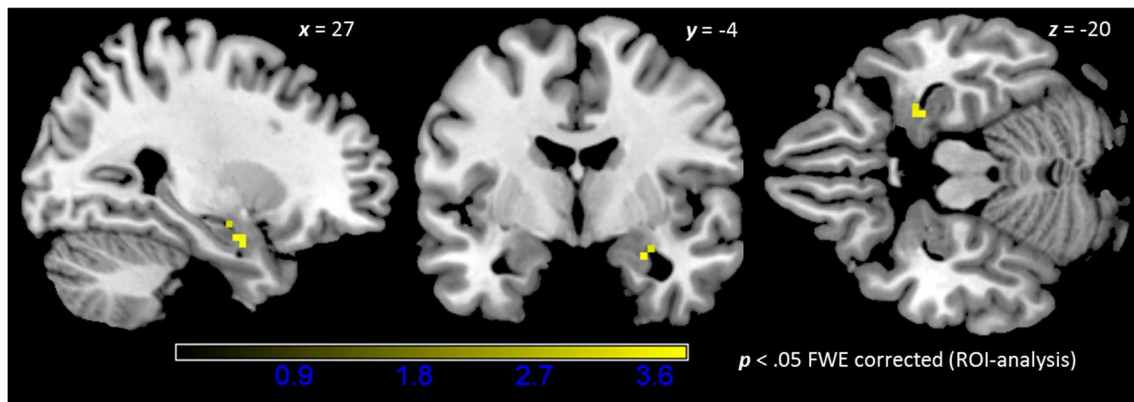


Fig. 7 Negative correlation between amygdala activity and cognitive flexibility scores during the reappraisal condition (ROI-analysis, $p < .05$ FWE corrected, $N = 20$)

correlate positively with reappraisal ability (hypothesis 1) and that WMC and cognitive flexibility performance are negatively correlated with brain activity in phylogenetically newer, lateral prefrontal regions (hypothesis 2a), but are positively correlated with brain activity in phylogenetically older prefrontal cortex regions (hypothesis 2b). Furthermore we expected to find a negative association between executive performance and amygdala activity during reappraisal (hypothesis 3). Our results showed that both WMC and cognitive flexibility performance were negatively correlated with prefrontal and subcortical brain activation during reappraisal. Interestingly, these findings not only held for phylogenetically newer but also for phylogenetically older brain regions. These associations were independent from reappraisal ability, given that neither WMC nor cognitive flexibility scores were significantly related with the amount of down-regulation. Hence, it seems that for achieving successful down-regulation of negative emotions, individuals with higher WMC and cognitive flexibility might need fewer neural resources in higher-order cognitive regions than individuals with lower WMC and cognitive flexibility. Furthermore, our results suggest that cognitive flexibility is negatively associated with the amount of amygdala activation during down-regulation of negative emotions by reappraisal. That means that the more cognitive flexibility, the lesser emotional limbic activation by distancing from negative stimuli.

Behavioral data

Reappraisal ability

We did not find significant correlations between WMC, cognitive flexibility, and reappraisal ability. Thus, WMC and cognitive flexibility performance have not significantly predicted the amount of down-regulation of negative stimuli

by self-focused reappraisal. This finding does not support hypothesis 1), and is not compatible with earlier work showing that higher WMC and higher cognitive flexibility performance are associated with better reappraisal abilities (Malooly et al. 2013; Schmeichel et al. 2008). However, these studies used film clips to induce negative emotions, which might be more challenging to reappraise and thus more sensitive to individual differences in reappraisal ability than pictures. It might also represent a power problem because of the small sample of $N = 20$ participants. Therefore, our results should be interpreted with caution and further studies should replicate these results with a larger sample in order to gain a deeper understanding of the mechanisms linking these executive functions and reappraisal ability.

Neural correlates of emotional reactivity and reappraisal

Emotional reactivity conditions activated frontal, temporal and limbic brain regions including the bilateral inferior frontal gyrus, medial prefrontal cortex, orbitofrontal cortex, right middle and superior temporal gyrus, amygdala and the insula. Furthermore, reappraisal activated structures of the frontoparietal network related to attentional processes (Menon 2011), including the right superior frontal gyrus, orbitofrontal cortex, bilateral middle frontal gyrus and inferior parietal gyrus. These findings are congruent with other reappraisal studies using a similar paradigm (Goldin et al. 2008; Kim and Hamann 2007; Koenigsberg et al. 2010; McRae et al. 2010; Ochsner et al. 2004).

Correlations between executive functions and reappraisal

Participants with lower WMC and lower levels of cognitive flexibility displayed higher activation in a number of phylogenetically older and newer prefrontal cortex regions.

WMC was negatively correlated with BOLD activity in the left middle frontal gyrus (BA 46/10) and right middle cingulate. Both middle frontal gyrus and middle cingulate are implicated in WMC (Geier et al. 2007; Leung et al. 2002; McNab and Klingberg 2008; Olesen et al. 2004). Moreover, the middle cingulate has been considered as an important region for reappraisal (Ochsner et al. 2004; Wager et al. 2008). Our findings thus raise the possibility that individuals with lower WMC use more neural resources associated to higher-order cognitive processes to down-regulate emotions via reappraisal.

Cognitive flexibility was negatively correlated with amygdala activation which is in accordance with hypothesis 3). Moreover, cognitive flexibility was negatively associated with the activation of the right inferior frontal gyrus during reappraisal, a region involved in cognitive inhibition (Hampshire et al. 2010; McNab et al. 2008; Muhlert et al. 2015) and tasks requiring some forms of cognitive flexibility (Hedden and Gabrieli 2010). This result points to the possibility that individuals with lower cognitive flexibility engaged more neural resources in brain regions associated to executive processing in order to yield a successful reappraisal.

The present findings also support hypothesis 2a), which suggested that WMC and cognitive flexibility performance are negatively associated with activity in phylogenetically newer prefrontal cortex regions. They are in line with other studies reporting that individuals with low WMC show overall higher prefrontal BOLD activity during WM tasks (Rypma et al. 2002; Rypma and D'Esposito 1999). Additionally, the results support earlier work on the scope of the neural correlates of executive functions. It was assumed that performing a novel task requires more effortful, controlled processing than when the task has been automatized through intense practice (Logan 1988; Shiffrin and Schneider 1977). Accordingly, extensive practice in cognitive tasks most commonly resulted in decreased prefrontal activity (Dahlin et al. 2008; Jansma et al. 2001; Kübler et al. 2006; Poldrack et al. 2005; Ramsey et al. 2004). Our results are congruent with these observations and suggest that high cognitive performance enables more efficient ER processing.

However, hypothesis 2b) of finding a positive correlation between cognitive performance and neural activation in phylogenetically older areas was not met. The hypothesis stemmed from observations by Schweizer et al. (2013), who documented additional activation of phylogenetically older regions after a WM training with emotional stimuli. Specifically, their results suggest that individuals with a higher WMC may have built stronger connections between cognitive and “key” ER areas, which would imply a greater efficiency of ER networks. Our results show, however, that neither WMC nor cognitive flexibility was positively correlated with neural activation of phylogenetically older regions during reappraisal. Yet, the association between performance

in executive functions and neural correlates of reappraisal may be different depending on whether these capabilities are individual differences or the result of preceding training. Perhaps solely intensive training in WMC and cognitive flexibility with emotional stimuli may eventually lead to a higher recruitment of phylogenetically older brain regions during reappraisal.

Limitations and future directions

The current study is not free of potential limitations. First, many of the reported neuroimaging findings should be interpreted with a degree of caution as they were based on small amounts of voxels. Furthermore, the considerably small sample size might have led to a poor overall signal to noise ratio. Moreover, it is likely that the limited number of trials per condition within the reappraisal task might have led to insignificant results as well. Therefore, results provide preliminary evidence for our hypothesis but further research is needed to replicate these results across larger numbers of subjects and with more trials. In contrast to previous studies, participants in the present study were part of a larger clinical study, i.e. they were older than the usual student population. Most participants also scored near the average of the sample in both executive tasks. Hence, we cannot rule out the possibility that the tests were not sensitive enough to detect differences between subjects. This caveat especially applies to the Trail Making Test, as it is a well suited instrument to distinguish between healthy individuals and patients suffering from brain impairments (Lezak 1995), but might not reliably differentiate within a healthy population. Finally, the social versus non-social nature of the stimuli presented may have confounded data on emotional reactivity during picture presentation. Despite these limitations, the results of the present study provide interesting perspectives for future investigations regarding the executive and neural underpinnings of reappraisal. We observed simultaneous activity in both phylogenetically older and newer regions, which were negatively associated to WMC and cognitive flexibility. This raises the intriguing possibility that phylogenetically older and newer prefrontal structures are perhaps more aligned when WMC and cognitive flexibility are low. Intensive training might therefore result in an activation shift from phylogenetically newer to older structures and subsequent spatially extended activation of phylogenetically older structures, as observed by Schweizer et al. (2013). Further investigations should examine this possibility by analyzing the neural correlates of reappraisal after training participants of different WMC and cognitive flexibility levels in executive control tasks.

In addition, our study sheds new light on the importance of cognitive flexibility in reappraisal, as the relationship between these two concepts has received comparably scant

attention in previous literature (Schmeichel and Tang 2014). The present results therefore encourage future researchers to investigate in more detail how cognitive flexibility processes aid the down-regulation of amygdala activation during reappraisal.

Concluding remarks

The present study adds important insights to the growing literature on executive functions involved in reappraisal. Firstly, results suggest that individuals with lower WMC and lower levels of cognitive flexibility might engage more neural resources of higher cognitive prefrontal regions to perform equally well in reappraisal compared to individuals with higher WMC and cognitive flexibility. Secondly, our study underscores the role of cognitive flexibility performance for the down-regulation of amygdala by reappraisal. Further research regarding practice effects and subsequent recruitment of phylogenetically older structures is needed to fully understand the dynamics of individual differences in executive functions, and their association with the neural correlates of reappraisal.

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Compliance with ethical standards

The manuscript meets the guidelines for ethical conduct and report of research mentioned in the 1964 Helsinki declaration and its later amendments. Informed consent was obtained from all individual participants included in the study. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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