

ORIGINAL ARTICLE

Brain Activity and Network Interactions Linked to Valence-Related Differences in the Impact of Emotional Distraction

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Abstract

Previous investigations showed that the impact of negative distraction on cognitive processing is linked to increased activation in a ventral affective system (VAS) and simultaneous deactivation in a dorsal executive system (DES). However, less is known about the influences of positive valence and different arousal levels on these effects. fMRI data were recorded while participants performed a working memory (WM) task, with positive and negative pictures presented as distracters during the delay between the memoranda and probes. First, positive distraction had reduced impact on WM performance, compared with negative distraction. Second, fMRI results identified valence-specific effects in DES regions and overlapping arousal and valence effects in VAS regions, suggesting increased impact of negative distraction and enhanced engagement of coping mechanisms for positive distraction. Third, a valence-related rostro-caudal dissociation was identified in medial frontal regions associated with the default-mode network (DMN). Finally, these DMN regions showed increased functional connectivity with DES regions for negative compared with positive distraction. Overall, these findings suggest that, while both positive and negative distraction engage partly similar arousal-dependent mechanisms, their differential impact on WM performance is linked to dissociations in the engagement of, and coupling between, regions associated with emotion processing and higher level cognitive control.

Key words: amygdala, anterior cingulate cortex, emotional interference, fronto-parietal network, salience network

Introduction

Investigations of the enhancing effects of emotion on episodic memory show that both pleasant (positive) and unpleasant (negative) stimuli are better remembered than the neutral ones (e.g., Dolcos et al. 2004b, 2011; Murty et al. 2010). This evidence suggests that the memory-enhancing effect of emotion is mainly driven by “arousal,” although effects of “valence” have also been identified (Kensinger and Corkin 2004; Mickley Steinmetz and Kensinger 2009; Mickley Steinmetz et al. 2010; Ritchey et al. 2011). However, less is known about the roles that arousal and

valence play in the impact of emotional stimuli on goal-oriented processing, when emotion is presented as task-irrelevant distraction. Previous investigations provided evidence for arousal- and valence-related effects linked to the emotional content manipulated in working memory (WM) (e.g., Kensinger and Corkin 2003; Levens and Phelps 2008; Lindstrom and Bohlin 2011), but it is not clear how such attributes of the emotional distracters interact with the maintenance of emotionally neutral content in WM. The present study investigated the roles of arousal and valence in the impact of emotional distraction on WM performance and the associated neural mechanisms. Clarification of these issues

is relevant for understanding both healthy functioning and alterations in clinical conditions associated with valence-related changes (Izard 2002; Forbes and Dahl 2005; Watson and Naragon-Gainey 2010; Gilbert 2012; Waugh and Koster 2014). Altered positive affect is involved in a range of clinical conditions, including depression, social phobia, schizophrenia, and bipolar disorder (Watson and Naragon-Gainey 2010), and hence can serve as a valid marker for symptoms associated with these disorders (Forbes and Dahl 2005; Gilbert 2012).

Valence (pleasantness) and arousal (intensity) are 2 basic dimensions commonly used to characterize the various forms of affect (Russell 1980, 2003; Lang et al. 1993; Russell and Barrett 1999). Although different models proposed over time have emphasized either one (e.g., valence; Watson and Tellegen 1985) or the other (e.g., arousal; Thayer 1989) of these 2 dimensions, most current approaches agree with a bidimensional structure, with valence varying from positive to negative and arousal from high to low (Larsen and Diener 1992; Lang et al. 1993; Russell and Barrett 1999; Russell 2003). In the context of experimental manipulations, however, valence and arousal may be more difficult to separate because stimuli used to induce positive and negative emotions typically determine also a change in arousal (Lindquist et al. 2015). Hence, it is not only important to employ positive and negative stimuli, but also to dissociate between different levels of arousal within the emotional categories (Shafer et al. 2011).

Based on previous findings regarding the memory-enhancing effect of emotion (Dolcos et al. 2004b; Murty et al. 2010), a default assumption regarding the impairing effect is that it may also be mainly driven by arousal (the “arousal account”). However, there is also evidence of valence-related differences in these effects (Kensinger and Corkin 2004; Mickley Steinmetz and Kensinger 2009; Mickley Steinmetz et al. 2010; Ritchey et al. 2011). Consistent with the existence of differences linked to the valence of emotional information, theories of motivational dispositions (Berntson et al. 1993; Cacioppo et al. 1997; Bradley and Lang 2007) and of positive affect (Ashby et al. 1999; Fredrickson 2001; Isen 2005) suggest that positive emotions and affective states are linked to different processing strategies, compared with negative ones and, hence, they may favorably influence cognition and behavior. Of note, emotional reactions and states are separable phenomena, with emotional reactions being relatively more intense and short in duration and states being relatively more prolonged, and they may exert different influences on cognition and behavior (Olsson and Öhman 2009). In the present work, we use “emotions” as referring to emotional reactions.

Although these perspectives jointly predict more favorable influences of positive compared with negative valence on goal-oriented processing, the available evidence so far has been mixed. Investigations focusing on processing emotional content in WM have provided equivocal results, showing either no consistent effects on WM performance (Kensinger and Corkin 2003), favorable influences on interference resolution (Levens and Phelps 2008), or performance facilitation irrespective of valence (Lindstrom and Bohlin 2011). On the other hand, investigations focusing on the impact of emotional distraction on WM maintenance have traditionally focused on negative valence (reviewed in Iordan, Dolcos, Dolcos, et al. 2013) and, thus, it is not clear whether positive stimuli may produce similar or different effects.

In contrast to these investigations targeting the effect of emotional reactions, studies examining the influence of affective states on WM performance have more consistently shown that positive affect facilitates controlled processing (Nadler et al.

2010; Carpenter et al. 2013; Yang et al. 2013; Brose et al. 2014; Storbeck and Maswood 2015). However, some investigations have identified enhancements only in certain domains, such as verbal WM and cognitive flexibility (Gray 2001; Dreisbach and Goschke 2004; Dreisbach 2006), whereas others have identified deleterious effects, similar to the impact of negative affect (Allen et al. 2014). Hence, it remains unclear what roles emotional valence and arousal play in influencing WM processing and, thus, the first main goal of the present investigation was to compare the impact of distracters with different valence and arousal properties on WM performance.

At the neural level, brain imaging studies in which emotional information was presented as transient distraction during WM tasks (Dolcos and McCarthy 2006; Dolcos et al. 2006, 2008, 2013; Anticevic et al. 2010; Denkova et al. 2010; Diaz et al. 2011; Oei et al. 2012; Iordan, Dolcos, Denkova et al. 2013) showed that the impairing effect of negative distraction was linked to opposing patterns of activity in 2 large neural systems: a “dorsal executive system” (DES) involved in cognitive/executive processing, showing decreased/disrupted activity, and a “ventral affective system” (VAS) involved in emotion processing, showing increased activity (reviewed in Dolcos et al. 2011; Iordan, Dolcos, Dolcos, et al. 2013). DES includes brain regions typically associated with cognitive control and maintenance of goal-relevant information, such as the dorsolateral prefrontal cortex (dlPFC) and the lateral parietal cortex (LPC) (Fuster 1997; Smith and Jonides 1999; D’Esposito et al. 2006; Koenigs et al. 2009; Nee et al. 2012; Niendam et al. 2012). VAS is a large aggregate which includes brain regions involved in basic emotion processing, such as the amygdala (AMY), regions involved in emotion integration and regulation, such as the ventrolateral prefrontal cortex (vlPFC), portions of the medial frontal cortex, as well as ventral regions susceptible to emotion modulation, such as visual cortex (Davidson and Irwin 1999; Davis and Whalen 2001; Phan et al. 2002; Seeley et al. 2007; Kober et al. 2008; Sergerie et al. 2008; Vytal and Hamann 2010; Dolcos et al. 2011; Lindquist et al. 2012).

Interestingly, the dorso-ventral dissociation between these 2 larger neural systems, identified in response to task manipulations with emotional distraction, overlaps with the main functional networks of the brain, identified based on their resting-state intrinsic connectivity. Specifically, the dlPFC and LPC areas mentioned above as part of DES have been associated with the “fronto-parietal” (FPN) or “central-executive” network (Seeley et al. 2007; Dosenbach et al. 2008; Bressler and Menon 2010; Yeo et al. 2011; Power and Petersen 2013). Turning to the VAS regions, the vlPFC is typically considered part of the “salience” (SN) or “ventral-attentional” network (Seeley et al. 2007; Corbetta et al. 2008; Bressler and Menon 2010) and has been associated with both processing of salient information (Seeley et al. 2007; Corbetta et al. 2008; Bressler and Menon 2010) and response inhibition (Aron et al. 2004, 2014; Aron 2007), and affect regulation (Kober et al. 2008; Vytal and Hamann 2010; Ochsner et al. 2012; but see Hampshire et al. 2010). Consistent with these functional associations, empirical evidence from studies of emotional distraction points to vlPFC involvement in both basic emotion processing and coping with distracting emotions (reviewed in Dolcos et al. 2011; Iordan, Dolcos, Dolcos, et al. 2013). The medial frontal areas of VAS, comprising the rostral and ventromedial prefrontal and ventral cingulate cortices (vmPFC/vACC) are an ensemble of subregions that have also been linked to both generation and modulation of emotion (Kober et al. 2008; Wager et al. 2008; Ochsner et al. 2012; Lindquist et al. 2015), as well as to self-referential processing (Northoff et al. 2006), and are typically considered part of the “default-mode network” (DMN) (Raichle et al.

2001; Greicius et al. 2003; Fox et al. 2005; Buckner et al. 2008). Interestingly, vmPFC/vACC regions have also been reported as being sensitive to different emotional properties of the stimuli linked to emotional arousal and valence (Wager et al. 2003, 2008; Dolcos et al. 2004a; Heinzel et al. 2005; Kensinger and Schacter 2006; Leclerc and Kensinger 2010; Straube et al. 2011; Schlottermeier et al. 2013; Kreplin and Fairclough 2013; Radua et al. 2014; Lindquist et al. 2015).

Importantly, the DES/VAS functional dissociation departs from the simple antagonism between bottom-up/ventral and top-down/dorsal systems (see Pfeifer and Allen 2012), by emphasizing the involvement of prefrontal VAS regions (e.g., vIPFC) in both emotion processing and control operations that enable emotion regulation and coping with distraction (Dolcos et al. 2006; Dolcos and McCarthy 2006; Denkova et al. 2010; Iordan, Dolcos, Dolcos, et al. 2013). Such dissociations have been systematically identified in tasks that have as a common denominator the clear perceptual and temporal segregation of goal-relevant and distracting information (see Banich et al. 2009), including emotional odd-ball tasks (Yamasaki et al. 2002; Wang et al. 2005) and emotional interrupt tasks (Mitchell et al. 2008), in addition to the delayed-response WM tasks employed by us and others. Of note, while we do not treat DES and VAS as equal to brain networks, we emphasize the possibility of overlaps between these larger neural systems sensitive to task-irrelevant emotional information and the large-scale functional networks. For instance, the task-induced dorso-ventral dissociation between DES and VAS resembles the dissociation between FPN/central-executive network and SN/ventral-attentional network, as identified by investigations employing resting-state functional connectivity (Dosenbach et al. 2007, 2008; Seeley et al. 2007; Power et al. 2011; Yeo et al. 2011).

An important emerging issue in the literature concerns identification of network interactions in response to task-related challenges (Smith et al. 2009; Lindquist and Barrett 2012; Barrett and Satpute 2013; Cole et al. 2014). In contrast to FPN and SN, which are considered “task-positive” networks, the DMN has been conceptualized as a “task-negative network” because it typically deactivates during cognitively demanding tasks (Fox et al. 2005). Increased functional connectivity between “task-positive” cognitive control regions and greater “anticorrelation” (i.e., negative correlation) between “task-negative” and “task-positive” brain regions have been linked to increased performance (Nee and Jonides 2008) and reduced variability in cognitive tasks (Kelly et al. 2007). In particular, it has been shown that the FPN is anticorrelated with DMN during the WM maintenance phase (Piccoli et al. 2015). In contrast, increased communication between “task-positive” and “task-negative” brain regions has been associated with performance decrements in cognitive tasks that engage the external environment (van Ast et al. 2014).

Although previous brain imaging investigations of emotional distraction identified specific brain regions involved in coping with emotional distraction (reviewed in Dolcos et al. 2011; Iordan, Dolcos, Dolcos, et al. 2013), they have focused mainly on negative distraction and have not identified network interactions in response to emotional distraction. Thus, the second main goal of the present study was to determine the neural correlates of the response to positive and negative distracters and to clarify whether their possibly differential impact on WM performance is linked to altered interactions between regions of FPN and DMN.

These issues were addressed here by investigating the contributions of emotional arousal and valence in the impact of emotional distraction on cognitive performance and the associated neural correlates. Behavioral assessments involved measures of

WM performance in the presence of high- and low-arousing positive and negative distraction. Brain activity was recorded using event-related fMRI, while healthy subjects performed the WM task with distraction. In order to clarify potential interactions between regions associated with the major brain networks, analyses of basic differences in brain activity were supplemented by functional connectivity analyses investigating task-induced dissociations in functional coupling between these regions. Based on the extant evidence, we made the following conditional predictions. If the distracting effects are mainly driven by arousal (arousal account), increased impact of high- compared with low-arousing stimuli was expected. On the other hand, if the distracting effects are sensitive to valence (valence account), diminished impact of positive compared with the negative distraction was expected (Berntson et al. 1993; Cacioppo et al. 1997; Bradley and Lang 2007). In the brain, we expected that differential impact of more versus less distracting conditions would be reflected in greater deactivation in DES regions and increased activity in VAS regions involved in emotion processing, for the more distracting condition. Moreover, increased activity in VAS regions involved in coping with emotional distraction was also expected, for the less distracting condition. Of note, the above predictions are not mutually exclusive and, hence, we also considered the possibility of interactions and/or effects consistent with both accounts. Thus, if the distracting effects of emotion are sensitive to both valence and arousal, then more subtle valence-related dissociations are expected in the context of overall arousal-driven responses, in both behavioral and brain imaging results. Finally, regarding interactions between “task-positive” regions associated with the fronto-parietal network and “task-negative” regions associated with the DMN, we expected that the detrimental impact of emotional distraction would be linked to increased functional coupling between “task-positive” and “task-negative” brain regions.

Materials and Methods

Subjects

A group of 18 healthy, young, right-handed women (18–34 years of age, average = 21.55, SD = 3.62) participated in the study. The rationale for including only female subjects in the present study was to maintain homogeneity in the subject sample, given previous evidence showing sex differences in the basic response to and coping with emotional distraction (Iordan, Dolcos, Denkova, et al. 2013). The subjects were screened for neurological and/or psychiatric disorders using a questionnaire developed in consultation with trained clinicians. The data from one participant were excluded from analyses because of large number of nonresponses during the WM task (i.e., more than 10% nonresponses). Hence, the reported behavioral and fMRI analyses are based on data from 17 subjects (average age = 21.65, SD = 3.7). The experimental protocol was approved by the Internal Review Board of the University of Illinois at Urbana-Champaign, and all subjects provided written informed consent.

Stimuli

The subjects performed a delayed-response WM task for faces with novel pictures presented as distracters during the delay interval between the memoranda and the probes (Fig. 1). The memoranda consisted of sets of 3 human faces (50% females/50% males) chosen to maximize similarities for increased task difficulty. The distracters consisted of pictures depicting pleasant



Figure 1. Diagram of the working memory (WM) task with emotional distraction. Functional magnetic resonance imaging (fMRI) data were recorded while subjects performed a WM task for faces, with distracters presented during the delay interval between the memoranda and the probes. The WM performance was measured using a recognition memory task, in which participants indicated by pushing a button whether single-face probes were part of the memoranda (Old = 1) or not (New = 2), and then they indicated their level of confidence (LOC) in their responses by pushing one of three buttons (1 = low, 2 = medium, 3 = high). All stimuli were presented in color. [Bottom wedding photos credits: Beercha (left) and Steve Evans (right). Licensed under Creative Common Attribution 2.0 Generic license (<https://creativecommons.org/licenses/by/2.0/deed.en>); last accessed: Oct 17, 2015). Pictures were converted to grayscale.]

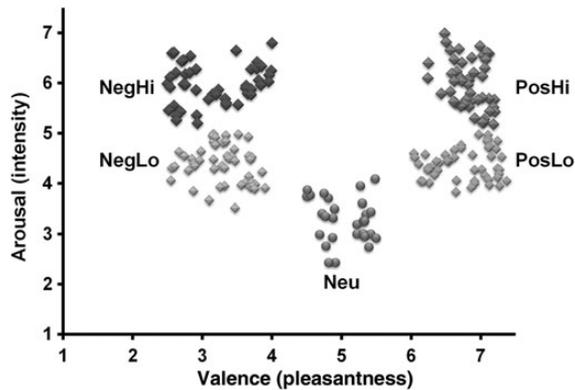


Figure 2. Distracter pictures in the valence \times arousal space. Five nonoverlapping categories of stimuli were selected from the International Affective Picture System (IAPS, Lang et al. 2008): negative high (NegHi) and low (NegLo) arousing, positive high (PosHi) and low (PosLo) arousing, and absolute neutral (Neu). High- and low-arousal emotional stimuli were matched for valence and negative and positive stimuli were matched for arousal.

(positive valence), unpleasant (negative valence), and neutral scenes (e.g., mundane activities) selected from the International Affective Picture System (IAPS, Lang et al. 2008) and supplemented from an in-house database for the neutral scenes. Two levels of arousal (high and low) were also considered for both positive and negative stimuli, to allow identification of potentially more subtle arousal effects within the emotional categories. In total, there were 5 categories of stimuli: negative high (NegHi) and low (NegLo) arousing, positive high (PosHi) and low (PosLo) arousing, and neutral (Neu) (Fig. 2). High- and low-arousal emotional stimuli were matched for valence and negative and positive stimuli were matched for arousal. The normative IAPS valence scores (mean; SD) for the emotional categories were as follows: NegHi (3.19; 0.51), NegLo (3.29; 0.37), PosHi (6.83; 0.25), PosLo (6.76; 0.41); Neu (4.99; 0.27). The normative IAPS arousal scores (mean; SD) for the emotional categories were as follows: NegHi (5.97; 0.39), NegLo (4.38; 0.38), PosHi (5.99; 0.48), PosLo (4.38; 0.31), Neu (3.56; 0.40). The valence \times arousal separation was confirmed by analyses of variance (ANOVAs). Within the emotional category, positive and negative pictures differed in terms of

their valence rating ($P < 0.001$) but not arousal ($P > 0.05$), whereas high- and low-arousing pictures differed in terms of their arousal ratings ($P < 0.001$) but not valence ($P > 0.05$). Furthermore, positive, negative, and neutral pictures differed in terms of their valence ratings (P 's < 0.001), and high-arousing, low-arousing, and neutral pictures differed in terms of their arousal ratings (P 's < 0.001). All selected stimuli depicted complex scenes, and there were no differences in visual complexity (as assessed by compressed file size, $F_{4,235} = 0.28$, $P = 0.893$) or luminance across the categories ($F_{4,235} = 1.17$, $P = 0.326$). Efforts were also made to match them as closely as possible for human presence and animacy across categories. Each picture was paired with its closest match in terms of arousal and valence properties, resulting in 120 pairs (24 pairs for each category). A total number of 144 trials (120 experimental trials plus 24 no-distraction control trials displaying a fixation cross) were involved. All stimuli were presented in color using E-Prime 1.0 (Psychology Software Tools, Pittsburgh, PA, USA).

Experimental Procedures

The pool of 144 trials was divided into 8 sets of 18 trials (counter-balanced across distracter-type categories), which were randomly assigned to 8 experimental blocks/runs. To avoid induction of longer lasting effects, the trials within each block were pseudo-randomized, so that no more than 2 consecutive trials of the same type were presented. To prevent possible biases resulted from using the same run order, participants were assigned different run orders; a total of 8 different run orders were involved. As illustrated in Figure 1, each trial started with the presentation of face memoranda (3.5 s), which subjects were instructed to encode and maintain in WM during the delay interval between the offset of the memoranda and the onset of the memory probe (12.5 s). Presentation of novel distracters started 2.5 s after the offset of the memoranda, and occurred for a total time of 6 s (3 s each). Participants were instructed to look at the distracters but maintain focus on the WM task, and then when the single-face probes appeared they had to indicate by a button press whether they were part of the current memorandum (Old) or not (New); 50% of the probes were Old and 50% were New. Subjects were instructed to make quick and accurate responses

while the probes were on the screen, and then they also rated the level of confidence (LOC) of their responses, using a 3-point Likert scale (1 = lowest, 3 = highest). The LOC rating was followed by a 10.5-s intertrial interval, to allow the hemodynamic response to return to baseline. During this time, participants were instructed to relax and refrain from doing anything systematically that could potentially affect the intertrial baseline signal (e.g., counting).

Imaging Protocol

Scanning was conducted on a 3-T Siemens Trio scanner. After the sagittal localizer and the 3D magnetization prepared rapid acquisition gradient echo anatomical images [repetition time (TR) = 1800 ms; echo time (TE) = 2.26 ms; flip angle = 9°; field of view (FOV) = 256 × 256 mm²; matrix size = 256 × 256 mm²; slice thickness = 1 mm; volume size = 192 slices; voxel size = 1 × 1 × 1 mm³], 8 blocks of 271 full-brain echo-planar functional images were acquired axially, co-planar with the anterior commissure - posterior commissure line (TR = 2000 ms; TE = 40 ms; flip angle = 90°; FOV = 256 × 256 mm²; matrix size = 64 × 64 mm²; slice thickness = 4 mm, no gap; volume size = 28 slices; voxel size = 4 × 4 × 4 mm³).

Behavioral Data Analyses

Responses in the WM task were classified in one of the four categories derived from signal detection theory (Macmillan and Creelman 1991): 1) “Hits,” corresponding to memorandum faces correctly classified as Old; 2) “Misses,” corresponding to memorandum faces incorrectly classified as New; 3) “Correct Rejections” (CRs), corresponding to new faces correctly classified as New; and 4) “False Alarms” (FAs), corresponding to new faces incorrectly classified as Old. Percentages of probes correctly identified as being Old or New were also calculated for each participant (% Correct = [% Hits + % CR]/2). Normality of % Correct data was assessed using the Shapiro–Wilk test. Differences in WM performance among the trial types were assessed using repeated-measures ANOVAs and follow-up t-tests, using SPSS. First, a 2 × 2 ANOVA (valence: positive, negative; arousal: high, low) was used to test for differences in WM performance within the emotional category. Then, one-way ANOVAs were used to test for valence and arousal effects individually, in the context of the 2 control conditions. Specifically, a one-way ANOVA (distraction type: positive, negative, neutral, and no-distraction) was used to test for valence effects, and similarly, a one-way ANOVA (distraction type: high-arousal, low-arousal, neutral, and no-distraction) was used to test for arousal effects.

fMRI Data Analyses

Statistical analyses were preceded by the following preprocessing steps (performed with SPM8 - Statistical Parametric Mapping): slice timing, realignment, motion correction, co-registration, normalization, and smoothing (8 mm kernel). For the data analysis, we used in-house custom MATLAB scripts involving whole-brain voxel-wise analyses (Dolcos and McCarthy 2006; Jordan, Dolcos, Denkova, et al. 2013) to compare the brain activity associated with the conditions of interest (e.g., trials with positive vs. negative distraction). For subject-level analyses, the fMRI signal was selectively averaged in each subject's data as a function of trial type (e.g., positive, negative, and control, for analyses concerning valence; and high-arousal, low-arousal, and control, for analyses concerning arousal; see also “Identification of Arousal- and Valence-Related Effects” below) and time point

(one prestimulus and 13 poststimulus onset time points). Pairwise t statistics for the contrasts of interest were calculated for each subject. No assumption was made about the shape of the hemodynamic response function because this method allows finer comparisons of the MR signal on a TR-by-TR basis and has been proven effective in dissociating responses produced by the WM task with emotional distraction (Dolcos and McCarthy 2006; Dolcos et al. 2008; Morey et al. 2009; Denkova et al. 2010; Jordan, Dolcos, Denkova, et al. 2013). The individual analysis produced whole-brain average and activation t maps for each condition, contrast of interest, and TR/time point.

The outputs of subject-level analyses were used as inputs for second-level random-effects within-group analyses. The analyses focused on effects observed at the peak time point (i.e., covering the 14–16 s period after the memoranda onset—TR 9), when the differential effects of the distracters are most evident (Dolcos and McCarthy 2006; Denkova et al. 2010; Jordan, Dolcos, Denkova, et al. 2013). For clarification purposes, in cases where there was a significant effect at TR 9 and the shape of the hemodynamic response suggested that the peak might have been shifted by 1 TR, we also investigated brain activity at ± 1 time point. Analyses were performed on correct trials (Hits and CR collapsed). This more stringent approach ensured that only instances where the subjects were performing the task were included in the analysis. Each random-effects t statistic map was corrected for multiple comparisons using a false discovery rate (FDR) of $q < 0.05$ (Genovese et al. 2002), unless otherwise specified as exception. Then, conjunction analyses were performed in MATLAB using the logical function AND, thus only voxels that met the threshold criteria in each of the contributing t maps survived the masking procedure. This procedure is consistent with the conjunction null hypothesis testing (Nichols et al. 2005). An extent threshold of 10 contiguous voxels was used in each of the contributing maps (Lieberman and Cunningham 2009).

A Priori Defined Functional Masks

Based on evidence regarding modulation of activity by emotional distraction in dorsal and ventral brain regions discussed above, on evidence showing differences in mPFC/vACC activity linked to the processing of emotional stimuli (Dolcos et al. 2004a; Heindel et al. 2005; Kensinger and Schacter 2006; Kreplin and Fairclough 2013; Radua et al. 2014), and on evidence identifying the mPFC as part of the DMN (Raichle et al. 2001; Buckner et al. 2008), 3 a priori functional masks were identified: the DES and VAS and the DMN. The DES and VAS maps were derived from the original study by Dolcos and McCarthy (2006), to identify modulation of activity by emotional distraction. That study used a similar WM task with high-arousing negative pictures as novel distracters, and thus for the purpose of the current study, 2 functional maps were used: Scrambled > Negative, to identify regions of DES, and Negative > Scrambled, to identify regions of VAS (see Supplementary Fig. 1). The contrasts between these 2 conditions were used (Scrambled vs. Negative) because these were the 2 most dissimilar conditions in terms of their impact on the WM performance (i.e., highest WM performance for scrambled and lowest for negative distraction) in the Dolcos and McCarthy (2006) study. As can be seen from Supplementary Figure 1, the brain regions identified for DES, for example (including dlPFC and LPC), map well with the fronto-parietal regions involved in WM processing, as identified by other sources. Furthermore, given that in the present study we also use positive stimuli, it was important to opt for the contrast that allowed identification of a more comprehensive map. The functional masks were calculated by merging suprathreshold brain activity in the

window from 12 to 16 s (TRs 8–9) after memoranda onset, which corresponds to the time interval when most of the peak effects reported by Dolcos and McCarthy (2006) in the 2 systems occurred, and were thresholded at $q < 0.05$ FDR-corrected. This ensured that the effects identified in the present study would be confined to regions showing the typical response to emotional distraction in the dorsal (i.e., increased deactivation) and ventral (i.e., increased activity) neural systems, based on an independent sample. To identify modulation of brain activity by emotional distraction in DMN regions, an a priori functional mask derived by meta-analysis performed with Neurosynth (Yarkoni et al. 2011) was used. The map was derived by an automated meta-analysis performed on studies indexed by the feature “default mode” (reverse inference map, thresholded at $q < 0.01$, FDR-corrected, which is the lowest default threshold in Neurosynth). Functional maps identifying response in the present study within each of these masks were thresholded at $q < 0.05$ FDR-corrected and 10 contiguous voxels.

Identification of Arousal- and Valence-Related Effects

The first main goal of the present study was to clarify the impact of emotional distraction on WM performance, by testing 2 competing accounts: the arousal and the valence accounts. This goal was accomplished by identifying DES, VAS, and DMN brain regions whose activity was sensitive to distracters with different arousal and valence properties, or their combination, both within the emotional categories and relative to control. To ensure an equal number of trials across conditions, both neutral and no-distraction control trials were collapsed into a single control condition (Ctrl). This was also justified by the absence of differences in WM performance between the 2 control conditions (neutral and no-distraction control; $t_{(16)} = 0.68$, $P = 0.507$; see also Table 1). These analyses are described in detail below. To identify brain regions whose activity was consistent with the arousal account, we performed analyses at 2 different levels, consistent with different conceptualizations of “arousal effects.” First, because more generic differences in arousal can be identified by comparing responses to emotionally arousing and neutral/control stimuli (Dolcos et al. 2004a), we tested for overlapping responses to both positive and negative distraction relative to control [i.e., overlapping deactivations in the dorsal system ($\text{Pos} < \text{Ctrl}$) \cap ($\text{Neg} < \text{Ctrl}$) and overlapping increased activity in the ventral system ($\text{Pos} > \text{Ctrl}$) \cap ($\text{Neg} > \text{Ctrl}$)]. Second, because more specific differences in arousal can be identified by comparing different arousal levels within the emotional category (Shafer et al. 2011), we directly compared brain activity related to high- and low-arousing emotional distraction and further masked with differences relative to control. Specifically, responses to high-arousing distraction were identified by deactivations in the dorsal system

($\text{AroHi} < \text{AroLo}$) \cap ($\text{AroHi} < \text{Ctrl}$) and increased activity in the ventral system ($\text{AroHi} > \text{AroLo}$) \cap ($\text{AroHi} > \text{Ctrl}$) relative to both low-arousing distraction and control. Similarly, responses to low-arousing distraction were identified by deactivations in the dorsal system ($\text{AroLo} < \text{AroHi}$) \cap ($\text{AroLo} < \text{Ctrl}$) and increased activity in the ventral system ($\text{AroLo} > \text{AroHi}$) \cap ($\text{AroLo} > \text{Ctrl}$) relative to both high-arousing distraction and control.

To identify brain regions whose activity was consistent with the valence account, we directly compared brain activity related to positive and negative distraction and further masked with differences relative to control. Specifically, responses to positive distraction were identified by deactivations in the dorsal system ($\text{Pos} < \text{Neg}$) \cap ($\text{Pos} < \text{Ctrl}$) and increased activity in the ventral system ($\text{Pos} > \text{Neg}$) \cap ($\text{Pos} > \text{Ctrl}$) relative to both negative distraction and control. Similarly, responses to negative distraction were identified by deactivations in the dorsal system ($\text{Neg} < \text{Pos}$) \cap ($\text{Neg} < \text{Ctrl}$) and increased activity in the ventral system ($\text{Neg} > \text{Pos}$) \cap ($\text{Neg} > \text{Ctrl}$) relative to both positive distraction and control. Because both the arousal- and valence-related analyses had 3 conditions, we opted for conjunctions between 2 separate pair-wise comparisons to test for effects similar to linear trends, but stricter (See <http://afni.nimh.nih.gov/sscc/gangc/Trend.html>, last accessed October 17, 2015). For instance, the conjunctions ($\text{AroHi} > \text{AroLo}$) \cap ($\text{AroLo} > \text{Ctrl}$) and ($\text{AroLo} > \text{AroHi}$) \cap ($\text{AroHi} > \text{Ctrl}$) identified linear effects of high and low arousal, respectively, and the conjunctions ($\text{Pos} > \text{Neg}$) \cap ($\text{Neg} > \text{Ctrl}$) and ($\text{Neg} > \text{Pos}$) \cap ($\text{Pos} > \text{Ctrl}$) identified linear effects of positive and negative valence, respectively. Finally, to identify brain regions whose activity was consistent with an interaction of both accounts, we tested for greater arousal effects for positive than negative distraction ($\text{PosHi} - \text{PosLo} > \text{NegHi} - \text{NegLo}$), and greater arousal effects for negative than positive distraction ($\text{NegHi} - \text{NegLo} > \text{PosHi} - \text{PosLo}$).

Functional Connectivity Analyses

To investigate modulation of functional relationships between targeted DMN and DES/VAS brain regions identified by the above analyses as showing valence-related sensitivity to emotional distraction (see Results section), functional connectivity analyses of delay activity among these regions were performed, using a procedure previously employed by Dolcos et al. (2006). This approach is similar to the “beta-series correlations” procedure described by Rissman et al. (2004), but uses the baseline-subtracted MR signal instead of beta values. For these analyses, at the first level, within-subject voxel-wise correlations were performed on a trial-by-trial basis, using as seeds activity extracted from 2 mPFC/vACC foci (i.e., peak and neighboring voxels), which were independently identified by the analyses above as showing differential sensitivity to positive and negative distraction (see

Table 1 Scores for working memory performance

	% Hits	% Misses	% False alarms	% Correct rejections	% Average correct
Positive	78.60%	21.40%	16.84%	83.16%	80.88%
Negative	71.91%	28.09%	20.61%	79.39%	75.65%
Positive and high arousal	78.65%	21.35%	13.46%	86.54%	82.60%
Positive and low arousal	78.55%	21.45%	20.23%	79.77%	79.16%
Negative and high arousal	68.94%	31.06%	14.48%	85.52%	77.23%
Negative and low arousal	74.88%	25.12%	26.74%	73.26%	74.07%
Neutral	79.28%	20.72%	24.87%	75.13%	77.21%
No distraction	69.25%	30.75%	16.67%	83.33%	76.29%

The text in bold font denotes the average WM scores in the presence of positive and negative distraction, regardless of arousal.

Results section), and targeting activity in DES and VAS regions. These trial-based analyses were performed for the time point of interest (TP 9), in each participant, for the 2 targeted trial types: i.e., trials associated with positive and negative distraction. The resulting correlation maps were normalized using Fisher's z transformation. At the second level, across subject random-effects t comparisons of the individual correlation maps were performed, to identify regions systematically showing greater functional connectivity with the seed regions, for one condition relative to the other (e.g., Neg > Pos). Because we targeted within-subjects differences in correlation strengths (e.g., increased correlations under negative compared with positive distraction), no other preprocessing steps were involved, aside from those performed for the analyses targeting differences in activation. Of note, the selection criterion for the seeds (i.e., differences in activation) did not bias the functional connectivity results because the seeds were selected based on the "average" response to Pos and Neg conditions, whereas the functional connectivity analysis used trial-by-trial estimates, which are independent of the average responses (Kinnison et al. 2012). This was confirmed by formal tests assessing whether average differences in brain activation were correlated with differences in functional connectivity (i.e., correlations) between targeted regions based on trial-by-trial data, using a procedure similar to Kinnison et al. (2012). Importantly, our approach was validated by a parallel analysis using "beta-series correlations" using the procedure described by Rissman et al. (2004). In brief, for this, we first created a general linear model in which the distracter phase of each trial was modeled individually by a separate covariate, yielding different parameter estimates for each trial and for each subject; the study (memoranda) and test (probe) phases of each trial, as well as the 6 motion parameters, were modeled as regressors of no interest. Then, seed-based correlations were calculated voxel-wise for each subject and each condition of interest (e.g., positive and negative distraction) using the same seed ROIs as above, and the resulting correlation maps were normalized using Fisher's z transformation. Similar to our procedure described above, random-effects t tests were used to detect voxels that showed increased coupling with the seed region for one condition relative to the other (e.g., Neg > Pos). Given our a priori hypotheses, these analyses were limited to activity in the targeted system (i.e., DES) and thresholded at a more liberal but accepted threshold of $P < 0.005$, uncorrected, and 10 contiguous voxels (Lieberman and Cunningham 2009).

Brain–Behavior Interaction Analyses

To identify brain regions whose activity was sensitive to individual variations in WM performance, brain–behavior relations were also investigated by calculating covariations between the fMRI signals in response to emotional distraction and WM performance. Negative brain–behavior covariations were expected to be indicative of processing leading to detrimental effects on WM performance, whereas positive covariations were presumed to be indicative of processing engaged to cope with distraction. These analyses were restricted within the a priori defined functional masks and involved investigation of covariations between WM performance and brain activity in 1) regions showing sensitivity to positive and/or negative distraction (increased or decreased activity) at the group-level average response, and 2) brain regions not showing differential sensitivity to positive and/or negative distraction at the group level; the latter analyses were justified by the fact that covariations with behavior can also be identified in the absence of significant differences observed

at the group level. The analyses performed to investigate brain–behavior relationships were based on calculating correlation maps identifying covariations between brain activity in the presence of distraction and scores indexing WM performance [i.e., % Correct = (% Hits + % CR)/2]. These analyses were thresholded at a more liberal but accepted threshold of $P < 0.005$, uncorrected, and 10 contiguous voxels (Lieberman and Cunningham 2009).

Results

Behavioral Results

Reduced Impact of Positive Distraction on WM Performance

Analyses of the WM data showed increased performance for positive compared with negative distraction, supporting the valence account. A summary of the responses in the WM task is presented in Table 1. First, the results of a two-way repeated-measures ANOVA (valence: positive, negative \times arousal: high, low) on WM performance for emotional distracters yielded a significant main effect of valence ($F_{1,16} = 6.74$, $P = 0.019$) with greater performance under positive (80.88%, $SD = 8.69$) than negative (75.65%, $SD = 8.89$) distraction. Because both the main effect of arousal ($F_{1,16} = 2.45$, $P = 0.137$) and the arousal \times valence interaction ($F_{1,16} = 0.004$, $P = 0.952$) were nonsignificant, high- and low-arousing trials were averaged for positive and negative valence, respectively (Table 1). Second, the results of a one-way repeated measures ANOVA (distraction type: positive, negative, neutral, and no-distraction control) on WM performance yielded a main effect of distraction ($F_{3,48} = 2.96$, $P = 0.041$), confirming the differential impact of positive and negative distraction also in the context of the 2 control conditions (neutral distraction and no distraction).

fMRI Results

Behavioral results showed that the impact of emotional distraction on cognitive performance is modulated by the valence of the task-irrelevant distraction. Analyses of fMRI data investigated the responses in brain activity linked to these behavioral findings (valence account), and/or whether it is also consistent with arousal-related responses (arousal account). Overall, these analyses yielded evidence consistent with both accounts. Consistent with the behavioral differences and the valence account, valence-driven differences were identified in DES and DMN regions and in their functional connectivity, in response to positive versus negative distraction. However, both valence- and arousal-driven effects were identified in VAS regions, in the absence of significant interactions between arousal and valence (Tables 2–4; see also the Materials and Methods section). These results are detailed below.

Dissociable and Overlapping Valence- and Arousal-Driven Effects in DES and VAS Regions

Consistent with both accounts, valence-related effects were identified in DES regions, and overlapping valence- and arousal-driven effects were observed in VAS regions. Consistent with the valence account, brain imaging results identified valence-related dissociations in both DES and VAS systems. Specifically, there was greater deactivation in LPC part of DES [right inferior parietal lobule (IPL), BA 40] under negative distraction, and increased activity in posterior vlPFC part of VAS (right IFG, BA 9, extending into the inferior frontal junction) under positive distraction (Fig. 3a,b). Furthermore, brain–behavior covariation analyses identified a more inferior vlPFC region (right IFG,

Table 2 Brain regions showing valence-driven effects

Brain regions	BA	Talairach coordinates			t Values		Cluster size
		x	y	z			
DES: greater deactivation to Neg					Neg < Pos	Neg < Ctrl	
LPC							
R inferior parietal lobule	40	43	-48	53	5.86	4.43	24
R inferior parietal lobule	7	35	-59	48	3.34	3.23	
PCC							
L/R cingulate gyrus	31	-5	-42	34	3.43	2.85	12
mOC							
L/R cuneus	7	-2	-68	32	5.19	4.25	45
VAS: increased activity to Pos					Pos > Neg	Pos > Ctrl	
mPFC							
L/R medial frontal gyrus	9	-5	56	29	4.43	6.39	83
vlPFC							
R inferior frontal gyrus	9	51	7	26	4.87	3.74	110
PrCG							
R precentral gyrus	6/4	50	-10	46	4.93	4.35	
PoCG							
R postcentral gyrus	2	54	-25	44	4.52	3.21	20
SPC							
R superior parietal lobule	7	20	-63	54	4.80	5.47	42
R precuneus	7	21	-58	37	3.62	3.44	
TOC							
L fusiform gyrus	37	-42	-44	-24	9.82	10.20	997
L fusiform gyrus	19	-45	-67	-15	7.90	9.88	
L middle temporal gyrus	37	-42	-58	3	4.26	5.43	
OC							
L middle occipital gyrus	18	-42	-79	-9	8.19	13.82	
L inferior occipital gyrus	18	-23	-87	-6	5.04	13.52	
L cuneus	19	-20	-84	34	5.69	5.25	
Cerebellum							
L declive		-23	-71	-15	4.60	8.27	
TOC							
R fusiform gyrus	37	40	-49	-16	8.58	9.96	1248
R fusiform gyrus	19	36	-76	-11	5.59	11.60	
R middle temporal gyrus	37	43	-55	5	6.40	6.41	
OC							
R middle occipital gyrus	18	28	-77	6	6.01	9.50	
R middle occipital gyrus	19	39	-70	4	5.61	7.77	
R cuneus	19	21	-87	31	4.99	6.13	
R lingual gyrus	18	25	-91	-6	6.30	16.51	
PCC							
L/R posterior cingulate	30/23	-5	-63	11	5.33	3.40	
Cerebellum							
R declive		17	-71	-15	4.95	7.07	
DMN: greater deactivation to Neg					Neg < Pos	Neg < Ctrl	
vmPFC/vACC							
L/R medial frontal gyrus/ Anterior cingulate	10/32	3	47	7	6.62	3.68	118
L/R anterior cingulate	32	-1	39	13	6.68	5.72	
LTC							
L middle temporal gyrus	21	-60	-15	-11	3.46	2.71	12
IPOC							
L angular gyrus	39	-42	-68	28	3.93	2.78	19
IPOC							
R angular gyrus	39	43	-65	33	3.71	3.55	18
PCC							
L/R cingulate gyrus	31	-2	-43	42	3.50	3.13	89
mPOC							
L/R precuneus	31	-2	-68	28	4.67	3.42	
mOC							
L/R cuneus	19	-2	-76	35	3.64	3.63	

Continued

Table 2 Continued

Brain regions	BA	Talairach coordinates			t Values		Cluster size
		x	y	z	Pos > Neg	Pos > Ctrl	
DMN: increased activity to Pos							
mPFC							
L medial frontal gyrus	9	-5	52	29	4.18	4.18	11
TPC							
L middle temporal gyrus	39	-46	-71	20	2.91	2.74	12
R superior temporal gyrus	39	47	-60	19	3.86	5.52	27
PCC							
L/R posterior cingulate	30/23	-5	-59	11	4.99	3.72	57
PHC							
L parahippocampal gyrus	30	-12	-47	5	3.69	2.73	

The table identifies brain regions showing valence-driven effects: i.e., specific increased or decreased responses to positive versus negative distraction. Effects in the dorsal executive system (i.e., specific deactivations for negative versus positive distraction), the ventral-affective system (i.e., specific increased activity for positive versus negative distraction), and the default-mode network (i.e., deactivations or increased activity for positive versus negative distraction) were masked with the corresponding a priori functional masks for DES, VAS, and DMN (see Materials and Methods). *T* values correspond to TR 9. Cluster size is in voxels. Significance threshold is $q < 0.05$ FDR-corrected.

LPC, lateral parietal cortex; PCC, posterior cingulate cortex; mOC, medial occipital cortex; mPFC, medial prefrontal cortex; vlPFC, ventrolateral prefrontal cortex; PrCG, precentral gyrus; PoCG, postcentral gyrus; SPC, superior parietal cortex; TOC, temporo-occipital cortex; vmPFC/vACC, ventromedial prefrontal/ventral anterior cingulate cortices; LTC, lateral temporal cortex; lPOC, lateral parieto-occipital cortex; mPOC, medial parieto-occipital cortex; TPC, temporo-parietal cortex; PHC, parahippocampal cortex; Pos, positive; Neg, negative; Ctrl, control; BA, Brodmann area; TR, repetition time.

BA 45/13, Talairach coordinates: $x = 40$, $y = 28$, $z = 9$) whose increased activity was linked to better performance for positive compared with negative distraction ($r = 0.78$, $P < 0.001$), in the absence of differences in activation between the 2 distracter categories at the group level (Fig. 3c). Overall, these findings are consistent with the behavioral results and suggest that the reduced impact of positive distraction on WM performance was associated with both reduced impact on DES regions (LPC) and superior recruitment of VAS regions (vlPFC) involved in coping with distraction, for positive compared with negative stimuli. Also, the findings regarding vlPFC activity and its relation to WM performance suggest both basic recruitment by salient stimuli and a role in coping with emotional distraction, consistent with its role as a “hub” in integrating emotional and executive processing.

Specific arousal-related effects were identified in both anterior and posterior vlPFC subregions (Table 3A), which showed both more generic (i.e., increased activity to both positive and negative distraction relative to control) and more specific arousal-driven effects (i.e., increased responses to high relative to both low-arousing emotional distracters and control). Although the arousal- and valence-related effects in the vlPFC partially overlapped, a relative segregation could also be observed, with valence-related effects being slightly more posterior and lateral than the arousal-driven effects (see Supplementary Fig. 2). Interestingly, both valence- and arousal-related responses in the right posterior vlPFC also showed patterns of activity consistent with linear effects [i.e., $(AroHi > AroLo) \cap (AroLo > Ctrl)$ for arousal and $(Pos > Neg) \cap (Neg > Ctrl)$ for valence] (see also the Materials and Methods section). To clarify the brain response in this region, percent signal change for each of the four emotional conditions was inspected individually, and the observed pattern of activity suggested that greater responses to positive valence were mainly driven by the high-arousing positive distracters, in the absence of a significant valence \times arousal interaction (see Supplementary Fig. 2). Finally, other regions showing both valence- and arousal-related effects included the visual areas, extending ventrally to the fusiform gyrus and dorsally to the superior parietal lobule (Table 4). Interestingly, only more generic arousal-driven effects

were identified in certain DES regions (anterior PFC and posterior LPC) and VAS regions (AMY, hippocampus, and thalamus), which showed similar decreased versus increased responses, respectively, to both positive and negative distracters (Table 3B). These responses occurred in the absence of specific dissociations between high- and low-arousing distraction, and are consistent with an overall sensitivity to emotional distraction, regardless of valence.

Valence-Related Rostro-Caudal Dissociation in DMN Regions

The results also identified dissociable patterns of response to positive and negative distracters in the mPFC/vACC, a brain region involved in both emotional and self-referential processing, and which is also part of DMN (Raichle et al. 2001; Fox et al. 2005; Buckner et al. 2008). Specifically, a more rostral mPFC area (BA 9), identified as part of both VAS and DMN, showed increased activity for positive distraction, whereas a more caudal mPFC/vACC area (BA 10/32), part of DMN, showed greater deactivation to negative distraction (Fig. 4). Interestingly, the peak response in the 2 regions occurred in slightly different time frames, with the deactivation to negative distraction in the more caudal region peaking earlier (TR 8–9) than the increased response to positive distraction in the more rostral region (TR 10). Taken together, these findings suggest an anterior-to-posterior dissociation in mPFC engagement and timing of activity, in response to task-irrelevant stimuli of opposing valence.

Valence-Related Dissociations in the Functional Connectivity of DMN and DES Regions

To further clarify the interactions between “task-positive” and “task-negative” brain regions showing valence-related effects, we performed functional connectivity analyses targeting the DES, VAS, and DMN areas identified above. These analyses were performed at the time point when the maximal impact of distraction on DES and VAS regions was identified (TR 9). Results showed increased functional connectivity between the 2 mPFC/vACC foci and parietal DES regions for negative compared with positive distraction (Fig. 5). Specifically, the more caudal mPFC/vACC (BA 10/32) area showing deactivation to negative distraction also showed

Table 3 Brain regions showing arousal-driven effects

Brain regions	BA	Talairach coordinates			t Values	Cluster size
		x	y	z		
A. Specific Arousal Effects						
DES: none						
VAS: increased activity to AroHi				AroHi > AroLo	AroHi > Ctrl	
vIPFC						
L inferior frontal gyrus	9	-38	4	27	4.50	4.97
L inferior frontal gyrus	44	-49	12	21	3.44	2.47
R inferior frontal gyrus	46	47	31	10	3.34	5.27
Inferior frontal gyrus	45/9	47	15	19	3.96	4.96
PCC						
L/R posterior cingulate	30/29	-5	-58	4	5.58	4.77
R posterior cingulate	23/30	10	-56	15	3.97	2.32
POC						
R precuneus	7	24	-59	48	3.93	6.32
TOC						
L fusiform gyrus	20	-38	-41	-13	4.31	9.93
L middle temporal gyrus	37	-49	-66	6	4.52	9.00
L inferior temporal gyrus	37	-49	-69	-1	4.53	8.42
OC						
L middle occipital gyrus	19	-35	-82	19	5.67	7.56
L cuneus	7	-24	-79	31	5.31	8.87
POC						
R precuneus	19	17	-81	42	3.28	4.42
R precuneus	31	24	-68	25	6.72	8.47
TOC						
R fusiform gyrus	37	43	-61	-6	4.65	8.35
R middle temporal gyrus	19	39	-75	18	7.70	10.69
R middle temporal gyrus	39	43	-70	11	6.90	10.52
R middle temporal gyrus	37	51	-58	5	5.48	8.13
R inferior temporal gyrus	19	47	-54	2	5.60	6.04
OC						
R cuneus	7	21	-72	32	5.45	5.51
Cerebellum						
L culmen		-30	-59	-25	4.52	5.49
L declive		-16	-71	-22	3.90	3.90
DMN: none						
B. Generic Arousal Effects^b						
DES: overlapping deactivations to Pos and Neg				Pos < Ctrl	Neg < Ctrl	
aPFC						
L middle frontal gyrus	10	-34	46	13	4.42	4.93
R middle frontal gyrus	10	40	41	25	4.05	5.87
LPC						
L superior parietal lobule	7	-43	-63	50	4.54	6.84
L inferior parietal lobule	40	-46	-54	36	4.16	8.65
R superior parietal lobule	7	39	-59	48	4.14	7.77
R inferior parietal lobule	39/40	39	-66	40	4.37	8.17
VAS: overlapping increased activity to Pos and Neg ^c				Pos > Ctrl	Neg > Ctrl	
MTL						
L amygdala		-23	1	-19	4.85	4.71
R amygdala		21	-8	-9	2.83	4.15
L hippocampus		-27	-23	-7	5.90	4.67
R hippocampus		25	-11	-16	5.09	2.43
Subcortical						
L thalamus		-16	-32	3	7.34	5.77
R thalamus		17	-28	4	6.67	6.24
DMN: none						

The table identifies (A) brain regions showing specific arousal-driven effects (i.e., specific increased or decreased responses to high- versus low-arousing distraction, regardless of their valence) and (B) additional brain regions showing only generic arousal-driven effects (i.e., overlapping responses to both positive and negative distraction, regardless of their arousal). Regarding (A), specific arousal-driven effects were targeted in the dorsal executive system (i.e., specific deactivations for high- versus low-arousing distraction), the ventral-affective system (i.e., specific increased activity for high- versus low-arousing distraction), and the default-mode network (i.e., deactivations or increased activity for high- versus low-arousing distraction). Regarding (B), additional generic arousal-driven effects were identified in specific DES (i.e., overlapping deactivations to both positive and negative distraction) and VAS (i.e., overlapping increased activity to both positive and negative distraction) regions. Similar to the findings reported in Table 2, these effects were masked by their corresponding a priori functional masks (see Materials and Methods). T values correspond to TR 9. Cluster size is in voxels. Significance threshold is $q < 0.05$ FDR-corrected.

vIPFC, ventrolateral prefrontal cortex; PCC, posterior cingulate Cortex; POC, parieto-occipital cortex; TOC, temporo-occipital cortex; OC, occipital cortex; aPFC, anterior prefrontal cortex; LPC, lateral parietal cortex; MTL, medial temporal lobe; AroHi, high arousal; AroLo, low arousal; Pos, positive; Neg, negative; Ctrl, control; BA, Brodmann area; TR, repetition time.

^aException (cluster size < 10 voxels).

^bAdditional regions which show generic but not specific arousal-driven effects.

^cSubcortical clusters were isolated using WFU PickAtlas/AAL (Tzourio-Mazoyer et al. 2002), and their sizes represent the number of active voxels within each anatomical region.

Table 4 Brain regions showing overlapping valence- and arousal-driven effects

Brain regions	BA	Talairach coordinates			t Values	Pos > Neg	Pos > Ctrl	AroHi > AroLo	AroHi > Ctrl	Cluster size
		x	y	z						
A. Overlapping valence and specific arousal effects										
DES: none										
VAS: overlapping increased activity to Pos and AroHi					Pos > Neg	Pos > Ctrl	AroHi > AroLo	AroHi > Ctrl		
vLPFC										
R inferior frontal gyrus	9	47	7	26	4.03	5.07	2.83	5.14	10	
SPC										
R superior parietal lobule	7	20	-63	54	4.80	5.47	2.91	4.65	25	
PCC										
L posterior cingulate	30	-5	-59	11	4.99	3.72	3.42	3.70	22	
TOC										
L fusiform gyrus	37	-38	-44	-24	9.26	9.63	2.87	9.15	33	
L fusiform gyrus	20	-34	-37	-16	4.87	8.38	3.56	7.50		
L middle temporal gyrus	19	-35	-78	20	2.41	5.67	5.16	6.89	178	
L middle occipital gyrus	19	-42	-74	9	4.27	7.58	3.78	6.70		
OC										
L cuneus	19	-20	-84	34	5.69	5.25	3.91	5.57		
POC										
R precuneus	31	24	-68	25	3.20	7.48	6.72	8.47	296	
R precuneus	19	17	-81	42	3.99	4.32	3.28	4.42		
TOC										
R middle temporal gyrus	37	43	-55	5	6.40	6.41	5.37	6.67		
R middle temporal gyrus	39	47	-70	11	4.45	8.74	6.11	10.46		
R fusiform gyrus	37	40	-49	-12	6.19	11.47	3.20	9.82		
R fusiform gyrus	19	40	-64	-10	5.73	10.34	3.09	9.86		
OC										
R cuneus	7	21	-76	32	4.87	5.52	4.76	5.46		
Cerebellum										
L culmen		-30	-59	-25	3.18	5.20	4.52	5.49	11	
DMN: none										
B. Overlapping valence and generic arousal effects^a										
DES: none										
VAS: overlapping increased activity to Pos and generic arousal response ^b					Pos > Neg	Pos > Ctrl	Neg > Ctrl			
MTL										
L hippocampus		-27	-23	-11	2.63	4.59	3.00		34	
R hippocampus		25	-11	-16	3.10	5.09	2.43		10	
Subcortical										
L thalamus		-16	-24	0	2.72	4.18	3.42		13	
DMN: none										

The table identifies brain regions showing overlapping valence and arousal effects: i.e., increased or decreased responses to positive versus negative distraction, in regions also showing (A) specific and (B) generic sensitivity to arousal, respectively (see Tables 2 and 3A,B). Also, similar to the findings reported in Tables 2 and 3, these effects were masked by their corresponding a priori functional masks (see Materials and Methods). T values correspond to TR 9. Cluster size is in voxels. Significance threshold is $q < 0.05$ FDR-corrected.

vLPFC, ventrolateral prefrontal cortex; SPC, superior parietal cortex; PCC, posterior cingulate Cortex; TOC, temporo-occipital cortex; POC, parieto-occipital cortex; OC, occipital cortex; Pos, positive; Neg, negative; AroHi, high arousal; AroLo, low arousal; Ctrl, control; BA, Brodmann area; TR, repetition time.

^aAdditional regions showing overlaps between valence and generic (i.e., not specific) arousal effects.

^bSubcortical clusters were isolated using WFU PickAtlas/AAL (Tzourio-Mazoyer et al. 2002), and their sizes represent the number of active voxels within each anatomical region.

increased connectivity with the LPC (right IPL, BA 40) for negative compared with positive distraction. Interestingly, the more rostral mPFC region (BA 9) whose response was strongest to positive stimuli also showed increased connectivity with the LPC for negative compared with positive distraction. Importantly, the parietal DES regions showing increased coupling with the mPFC also showed greater deactivation to negative distraction (see Table 2). To ensure that the selection criterion for the functional connectivity seeds (i.e., differences in activation) did not bias the results, we formally tested whether average differences in brain

activation were correlated with differences in functional connectivity (i.e., correlations) between targeted regions based on trial-by-trial data, using a procedure similar to Kinnison et al. (2012). Results showed an absence of a relationship between differences in activation and differences in functional connectivity for both rostral mPFC-LPC ($r = -0.08$, $P = 0.77$) and caudal mPFC/vACC-LPC ($r = -0.05$, $P = 0.85$) pairs. Hence, the selection criterion did not bias the functional connectivity results. Additionally, these findings were also replicated by analyses performed with an alternative method, using "beta-series correlations" (Rissman

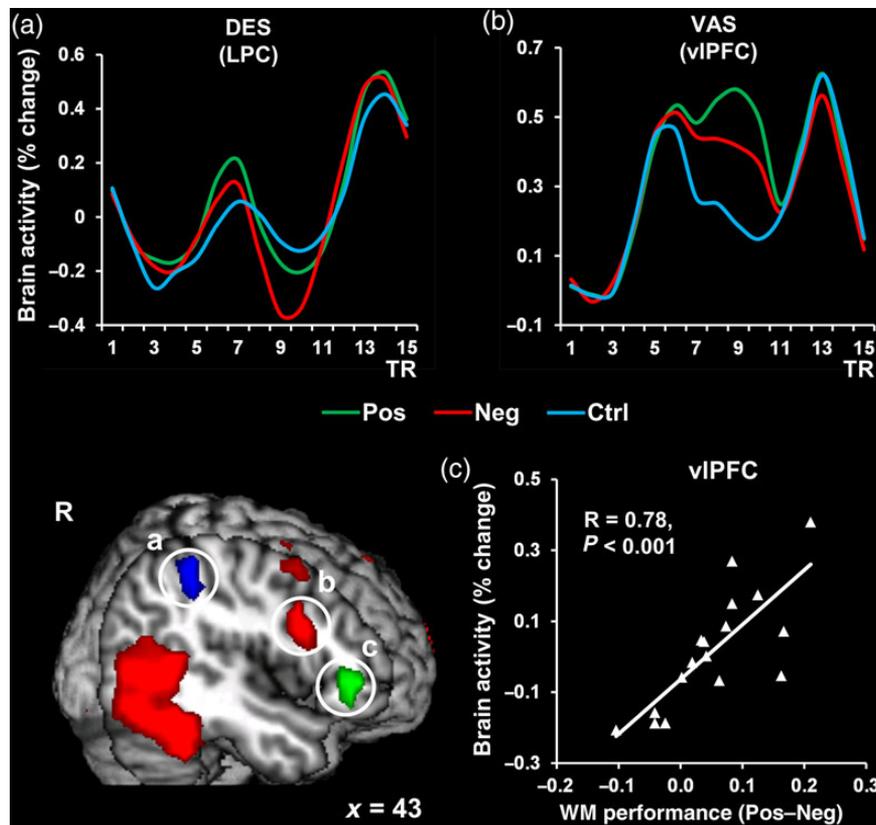


Figure 3. Valence-related differences in the activity of DES and VAS regions. Negative distraction was associated with greater deactivation in (a) DES regions (LPC, blue area), whereas positive distraction was associated with increased activity in (b) VAS regions (vIPFC, red area). Also, increased activity in a more inferior vIPFC subregion (c, green area) was associated with increased WM performance for positive relative to negative distraction. Of note, valence effects overlapped with arousal-driven responses in the vIPFC (b and see [Supplementary Fig. 2](#)). The line graph in (a) displays the time course of brain activity extracted from the peak voxel of the Pos versus Neg comparison (Talairach coordinates: $x = 43$, $y = -48$, $z = 53$). The line graph in (b) displays the time course of brain activity extracted from the peak voxel of the overlap between the Pos versus Neg comparison and HiAro versus LoAro comparison in the vIPFC (see main text and [Supplementary Fig. 2](#); Talairach coordinates: $x = 47$, $y = 7$, $z = 26$). The scatterplot in (c) displays the brain-behavior covariation extracted from the peak voxel of the correlation (Talairach coordinates: $x = 40$, $y = 28$, $z = 9$) (two-tailed). The maps showing differences in activity are displayed at $q < 0.05$ FDR-corrected, and the map showing the brain-behavior covariation is displayed at $P < 0.005$. DES, dorsal executive system; VAS, ventral affective system; LPC, lateral parietal cortex; vIPFC, ventrolateral prefrontal cortex; Pos, positive; Neg, negative; Ctrl, control; WM, working memory; TR, repetition time (2 s); R, right.

[et al. 2004](#)). Overall, these findings suggest increased functional coupling between DMN and FPN for negative distraction, which was also the condition associated with lower WM performance.

Discussion

The goal of the present study was to clarify the roles of arousal and valence in the impact of emotional distraction on WM performance, by testing 2 competing accounts: the arousal and valence accounts. There were 4 main findings. First, consistent with the valence account, behavioral results showed reduced impact of positive compared with negative distraction on WM performance. Second, brain imaging results identified valence-specific effects in DES regions (LPC) and overlapping arousal- and valence-driven effects in VAS regions (vIPFC). Additionally, a valence-related rostro-caudal dissociation was identified in medial frontal regions (mPFC/vACC) part of DMN, with the rostral subregion showing increased response to positive and the caudal subregion showing greater deactivation to negative stimuli. Finally, there was a valence-related dissociation in functional coupling, with DMN regions (mPFC/vACC) showing increased functional connectivity with DES regions (LPC) for negative compared with positive distraction. These findings are discussed in turn below.

Reduced Impact of Positive Distraction on WM Performance

The present findings showing reduced impact of positive distraction on WM performance support the valence account, and suggest that subjects were better able to cope with positive compared with negative distraction. Theories of motivational dispositions ([Berntson et al. 1993](#); [Cacioppo et al. 1997](#); [Bradley and Lang 2007](#)) suggest that although both positive and negative stimuli are relevant for survival, positive stimuli have different significance and are usually less imperative than the negative ones. According to these theories, organisms display both a “positivity offset” which encourages approach and exploration at low motivational levels, as well as a “negativity bias” which enables the abrupt engagement of defense systems when a threat signal is detected. Importantly, negative reactions tend to be stronger than the positive ones because the consequences of potential threats typically far exceed those of unpursued opportunities ([Berntson et al. 1993](#); [Cacioppo et al. 1997](#); [Bradley and Lang 2007](#)). For example, the immediate consequences of not readily paying attention to a food source or a potential mating partner are usually less dramatic than the consequences of not paying attention to a predator.

Hence, under conditions of goal-oriented processing, task-irrelevant positive stimuli are better controlled compared with the

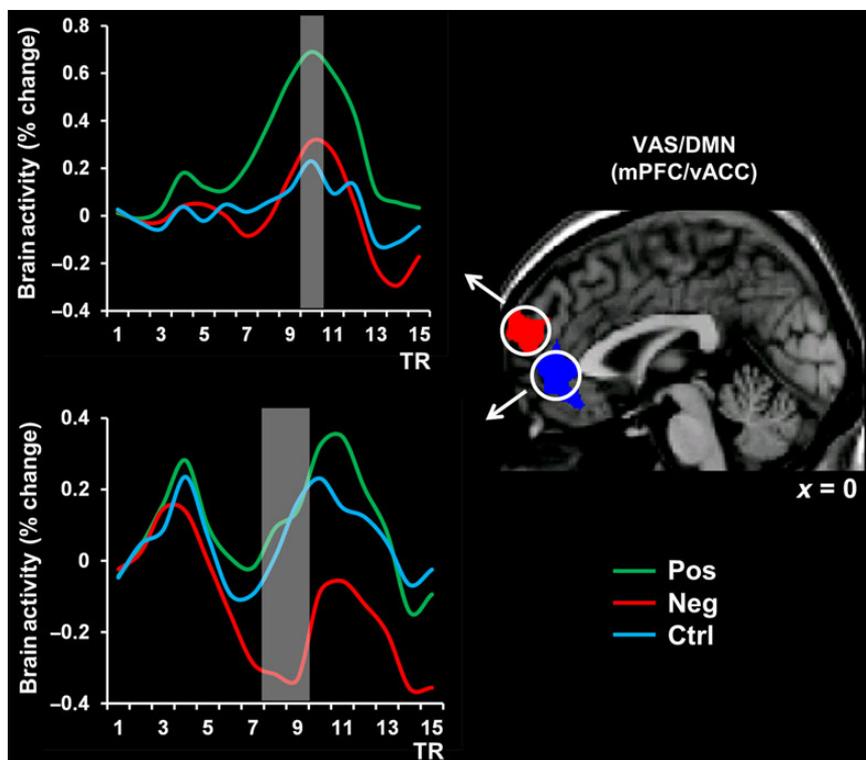


Figure 4. Rostro-caudal dissociation in the medial frontal cortex in response to positive and negative distraction. A more rostral mPFC area (BA 9, red area) showed increased activity for positive distraction, whereas a more caudal mPFC/vACC area (BA 10/32, blue area) showed specific deactivation to negative distraction. The line graphs display the time course of brain activity extracted from the peak voxel of the Pos versus Neg comparison (Talairach coordinates: $x = -5, y = 56, z = 29$ for the red area, and $x = 3, y = 47, z = 7$ for the blue area). The gray rectangles highlight the time points (TRs) when the peak difference between Pos and Neg distraction-related activity occurred. All maps are displayed at $q < 0.05$ FDR-corrected. mPFC/vACC, medial prefrontal cortex/ventral anterior cingulate cortex; Pos, positive; Neg, negative; Neu, neutral; Ctrl, control; TR, repetition time (2 s).

negative ones and, thus, negative distracters are more interfering with on-going cognitive performance, even at similar levels of arousal. Additionally, positive affect has also been associated with “broadening” the scope of attention and with flexible integration of information (Fredrickson 2001, 2004; Fredrickson and Branigan 2005). This is in contrast with the influence of negative affective states on cognitive performance, which have often been associated with deleterious effects (reviewed in Mitchell and Phillips 2007), probably due to fostering intrusive thoughts and ruminations that detract from goal-oriented processing (Eysenck et al. 2007). Although emotional reactions and states are separable phenomena and they may exert different influences on cognition and behavior (Olsson and Öhman 2009), it is plausible that potential interference from positive distraction may be compensated by facilitatory effects that would allow maintaining the memoranda in WM while still processing the distracters. These results are also in line with recent evidence suggesting facilitation of controlled processing by positive affect (Nadler et al. 2010; Carpenter et al. 2013; Yang et al. 2013).

The present findings extend previous investigations of the impact of emotional distraction on WM maintenance, which have focused on negative valence (Jordan, Dolcos, Dolcos, et al. 2013), and other investigations focusing on arousal- and valence-related effects linked to the emotional content manipulated in WM (Kensinger and Corkin 2003; Levens and Phelps 2008; Lindstrom and Bohlin 2011). It should be noted, however, that findings from these 2 main types of paradigms may not be directly comparable because of their conceptual and methodological differences. That is, in one case emotional distraction presented during the interval between the memoranda and probes can be perceptually and temporally segregated from the neutral WM content, whereas in the other case emotional information is part of the content of

information manipulated in WM (see Banich et al. 2009). At any rate, as discussed below, analyses of fMRI data identified for the first time patterns of responses consistent with the behavioral findings, with valence-related effects in brain activity specific to DES regions and overlaps with arousal-driven effects in VAS regions.

Dissociable and Overlapping Valence- and Arousal-Driven Effects in DES and VAS Regions

The findings showing greater deactivation to negative distraction in DES regions (LPC) and increased activation to positive distraction in VAS regions (vIPFC) suggest both greater detrimental impact of negative distraction on mechanisms supporting WM and increased recruitment of coping mechanisms for positive distraction. The present DES results are consistent with previous findings linking greater deactivation in fronto-parietal areas to the interfering effect of emotional distraction on WM performance (Dolcos et al. 2006, 2008, 2013; Dolcos and McCarthy 2006; Anticevic et al. 2010; Denkova et al. 2010; Diaz et al. 2011; Oei et al. 2012; Jordan, Dolcos, Denkova, et al. 2013). Also, the LPC is the posterior “hub” in the fronto-parietal executive network, which also includes the dlPFC (Dosenbach et al. 2006, 2007, 2008; Seeley et al. 2007; Power et al. 2011; Yeo et al. 2011; Power and Petersen 2013). Increased activity in these regions has been implicated in active maintenance of task-relevant information (Fuster 1997; Smith and Jonides 1999; Hopfinger et al. 2000; Corbetta and Shulman 2002; D’Esposito et al. 2006; Koenigs et al. 2009; Nee et al. 2012; Niendam et al. 2012). It has been suggested that the role of LPC in WM processing is related to top-down biasing in order to foreground in WM the representation that is the focus of attention (Nee and Jonides 2008). Given their increased

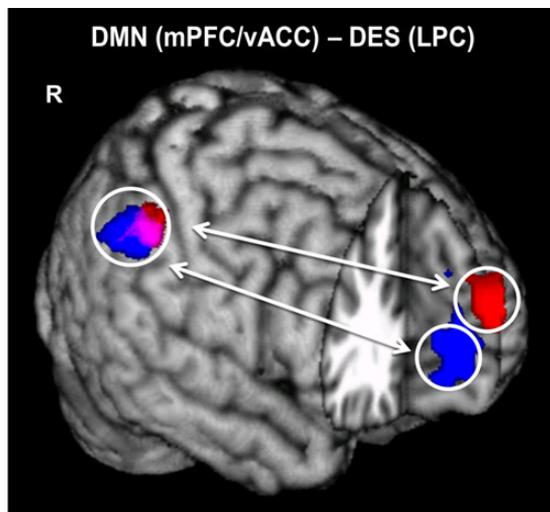


Figure 5. Valence-related dissociations in functional connectivity between DMN and DES regions. The 2 mPFC subregions, part of the default-mode network (DMN), showing valence-related effects (see Fig. 4) also showed increased functional connectivity with LPC, part of the dorsal executive system (DES), under negative distraction. Both rostral (red) and caudal (blue) medial frontal sub-regions showed increased connectivity with the LPC areas (red and blue areas, respectively; overlap displayed in magenta), which showed deactivation to negative distraction. The maps showing differences in activation are displayed at $q < 0.05$ FDR-corrected, and the maps showing functional connectivity are displayed at $P < 0.005$. LPC, lateral parietal cortex; mPFC/vACC, medial prefrontal cortex/ventral anterior cingulate cortex.

imperativeness (Berntson et al. 1993; Cacioppo et al. 1997; Bradley and Lang 2007), negative stimuli may interfere more with this process compared with positive stimuli, and hence disrupt WM.

The overlapping arousal- and valence-driven responses in the posterior vIPFC, in the absence of significant arousal \times valence interactions, indicate that the contributions of valence and arousal in this region are additive rather than interactive. At the same time, the involvement of this region in processing distracters with different emotional attributes and behavioral outcomes is consistent with its putative role as a “hub” in processing salient information (Seeley et al. 2007; Corbetta et al. 2008; Bressler and Menon 2010). On the other hand, a relative segregation of responses in the vIPFC, with the valence-related effects being slightly more posterior and lateral than the arousal-driven effects, suggests also potential subregional specificity and dissociations within the IFG.

Of note, increased activity in the vIPFC has previously been linked to both increased WM performance and reduced distractibility (Dolcos and McCarthy 2006; Dolcos et al. 2006; Jordan, Dolcos, Dolcos, et al. 2013). Consistent with this interpretation, the vIPFC has also been proposed as a site of cross-modal inhibition, being generally associated with inhibitory processes (Aron et al. 2004; Aron 2007; Berkman et al. 2009) and inhibition of negative emotion (Petrovic et al. 2002; Ochsner et al. 2004). The interpretation that increased vIPFC activity for positive distraction reflects better engagement of coping with distraction mechanisms is further supported by the results of our brain–behavior covariation analyses, showing that subjects who engaged this region more in response to positive than negative distraction also performed better in the WM task. Of note, while these results are consistent with the idea of “functional heterogeneity” in the vIPFC area (Levy and Wagner 2011; Cai et al. 2014; Warren et al. 2014; see also Power et al. 2011; Gordon et al. 2014), operational distinctions between “salience” and “inhibition” are not always clear-cut, as salient or unexpected stimuli may also recruit some form of inhibitory processing (see Hampshire et al. 2010; Aron et al. 2014; Kohn et al. 2014).

Overall, the task-induced dorso-ventral dissociation between DES and VAS resembles the dissociation between FPN/central-executive network and SN/ventral-attentional network, as identified in studies assessing resting-state functional connectivity (Dosenbach et al. 2007, 2008; Seeley et al. 2007; Power et al. 2011; Yeo et al. 2011). Although there are important methodological differences between these 2 approaches (Buckner et al. 2013), the basic configuration of the major brain networks is relatively stable across both task-related recordings and resting-state (Cole et al. 2014). Furthermore, this raises the possibility of overlaps between VAS regions and regions attributed to SN (Seeley et al. 2007; Lindquist and Barrett 2012; Lindquist et al. 2015; Touroutoglou et al. 2015). It should be noted, however, that dissociations can also be identified. For instance, both the ventral attention and cingulo-opercular networks converge in the vIPFC, and they have been linked to stimulus-driven orienting of attention and sustained task-set maintenance, respectively (Corbetta et al. 2008; Dosenbach et al. 2008). Whereas a formal testing of this hypothesis was beyond the scope of the present investigation, identification of more subtle networks-based dissociations within these larger neural systems in future research is plausible and important. Given recent evidence for functional heterogeneity in the vIPFC (Levy and Wagner 2011; Power et al. 2011; Cai et al. 2014; Gordon et al. 2014; Warren et al. 2014), investigation of functional dissociation in this area by combining task manipulations and resting-state recordings seems to be a promising avenue for future research.

Valence-Related Rostro-Caudal Dissociation in DMN Regions

The findings showing overall increased activity to positive distraction in rostral and ventral mPFC/vACC are consistent with the general involvement of this region in encoding positive value (Wager et al. 2003; Dolcos et al. 2004a; Kensinger and Schacter 2006; Leclerc and Kensinger 2010; Straube et al. 2011; Schlochtermeyer et al. 2013; Kreplin and Fairclough 2013) and self-referential processing (Raichle et al. 2001; Northoff et al. 2006; Cabeza and St Jacques 2007; Schacter et al. 2007; Wager et al. 2008; Ochsner et al. 2012; Denkova et al. 2015) and suggest greater self-engagement in the processing of positive stimuli. The mPFC/vACC region (BA 10/32) has been associated with both DMN (Raichle et al. 2001; Fox et al. 2005; Buckner et al. 2008) and emotion processing (Lindquist et al. 2012, 2015; Roy et al. 2012), and in particular shows an overall affinity for positive affect (Lindquist et al. 2012, 2015). Although early perspectives (Bush et al. 2000) have operated a distinction between dorsal-caudal cognitive and ventral-rostral affective mPFC/ACC regions, later evidence has suggested that both regions contribute to emotion processing, with the dorsal-caudal region involved mainly in evaluative operations and the ventral-rostral region involved mainly in regulatory functions (Etkin et al. 2011).

Interestingly, the present findings point to a rostro-caudal dissociation in both sensitivity and timing of the response to positive versus negative distraction, suggesting differences in functional specialization between the 2 mPFC/vACC subregions. The differential sensitivity to positive versus negative stimuli suggests differences in encoding the approach versus avoidance value of emotional stimuli (Wager et al. 2003). This finding is also consistent with previous evidence showing valence-related effects in mPFC/vACC (Nielen et al. 2009; Vrticka et al. 2011) and specific deactivations in response to negative (disgusting) images (Radua et al. 2014) and negative words (Richter et al. 2010). This valence-related anterior-to-posterior dissociation complements a previously observed dorsal-ventral dissociation in mPFC activity in response to the arousal and valence properties of emotional

stimuli, albeit under different task conditions (i.e., using a single, not dual, task) (Dolcos et al. 2004a; Kensinger and Schacter 2006). Of note, mPFC/vACC is also part of the DMN (Raichle et al. 2001; Fox et al. 2005; Buckner et al. 2008), which comprises so-called task-negative regions whose deactivation is required in order to better perform tasks that require interactions with the external environment (Fox et al. 2005). Hence, it is possible that greater deactivation in this region to negative distraction may reflect increased (though unsuccessful) attempts at re-orienting toward the WM task under increased interference by negative distraction.

The difference in timing along the rostral-caudal axis is consistent with a proposed gradient of processing complexity in the mPFC (Olsson and Ochsner 2008; Roy et al. 2012). Specifically, the posterior division, including the ventromedial PFC, is thought to be part of the “affect generation” subsystem and involved in more simple operations linked to the processing of “first-order” body state information, whereas the anterior division, including the rostral mPFC, is thought to be part of the “simulation” subsystem, and involved in complex or integrative operations such as re-representation of information and mentalizing (Olsson and Ochsner 2008; Roy et al. 2012). In this view, the earlier response in the caudal mPFC/vACC region may reflect its involvement in an initial reaction to the sensory qualities of negative information, whereas the delayed response in the rostral mPFC may reflect involvement in the subsequent elaboration of positive information. However, given that the time resolution of fMRI analyses is typically too coarse for subtle timing-related distinctions, these results should be treated with caution.

Valence-Related Dissociations in Functional Connectivity of DMN and DES Regions

The findings showing increased functional connectivity between mPFC and DES regions for negative distraction suggest task-induced changes in communication between DMN and FPN regions. Increased functional connectivity between mPFC and LPC under higher impact by negative distraction suggests a potential interference of affective information integrated by the mPFC with goal-relevant representations maintained by the fronto-parietal network. Activity in DMN, which includes the mPFC, is typically negatively correlated with activity in the fronto-parietal network (Fox et al. 2005), and in particular during the maintenance phase of WM processing (Piccoli et al. 2015). On the other hand, a reduction in the negative relations between medial prefrontal and parietal regions has been linked to adverse effects of socio-emotional stress (van Ast et al. 2014). Furthermore, the present results suggest that increased DMN-FPN communication occurred independently of the individual selectivity of the more anterior mPFC subregion for positive distraction. Although the more anterior mPFC region showed specific increased activity to positive distraction, it also showed increased functional connectivity with LPC for negative distraction. Importantly, parietal regions showing increased functional connectivity with the mPFC were also more impacted by negative distraction, as reflected in the patterns of deactivation to negative distraction in LPC (BA 40). Overall, these findings point to increased communication between the DMN and FPN under interference by negative distraction, as a mechanism by which goal-irrelevant negative emotions impact on-going cognitive performance.

Caveats

One limitation of the present study is that only female participants were involved, which reduces the generalizability of our results. However, given sex differences in the response to

emotional stimuli and emotional distraction (Lang et al. 1993; Hamann and Canli 2004; Domes et al. 2010; McRae et al. 2010; Jordan, Dolcos, Denkova, et al. 2013), this was important for maintaining homogeneity in the subject sample. Another limitation is that the hormonal state of our subjects was not assessed, and this may have potentially influenced their emotional reactivity (see Sundstrom Poromaa and Gingnell 2014).

Conclusions

In summary, the present findings clarify the roles of arousal and valence in the impact of emotional distraction on WM, by identifying for the first time valence-related dissociations in the response and interactions between brain regions associated with executive and emotion processing. Consistent with the idea of a facilitating effect of positive emotion on controlled processing posited by theories of motivational dispositions (Bertson et al. 1993; Cacioppo et al. 1997; Bradley and Lang 2007) and of positive affect (Ashby et al. 1999; Fredrickson 2001; Isen 2005), our results show that positive distraction is associated with both reduced cognitive interference and better coping compared with negative distraction. The present fMRI findings identified both reduced impact of positive distraction on dorsal brain regions (LPC), part of the fronto-parietal network, and superior recruitment of ventral regions (e.g., vlPFC), part of the salience network, as well as valence-related dissociations in medial frontal areas, part of the default-mode network (mPFC/vACC). Moreover, there were different patterns of connectivity between regions of the default mode and fronto-parietal networks, for negative versus positive distraction. Overall, these findings show that, although positive and negative distraction may engage partly similar arousal-dependent mechanisms, their differential impact on concurrent cognitive performance is linked to valence dissociations in the engagement of and coupling between regions associated with basic emotion processing and higher level cognitive control. Collectively, the present study provides initial fMRI evidence regarding the role of valence in the impact of emotional distraction on WM performance, and has implications for understanding affective disorders, which are characterized by increased susceptibility to negatively valenced distraction and diminished processing of positive emotions (e.g., anhedonia in depression) (Izard 2002; Forbes and Dahl 2005; Watson and Naragon-Gainey 2010; Gilbert 2012; Waugh and Koster 2014).

Supplementary material

Supplementary Material can be found at <http://www.cercor.oxfordjournals.org/> online.

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Notes

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