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Tracking the effect of emotional distraction in working memory brain networks: Evidence from an MEG study

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Abstract

The active maintenance of information in visual working memory (WM) is known to rely on the sustained activity over functional networks including frontal, parietal, occipital, and temporal cortices. Previous studies have described interference-based disturbances in the functional coupling between prefrontal and posterior cortices, and that such disturbances can be restored for a successful WM performance after the presentation of the interfering stimulus. However, very few studies have applied functional connectivity measures to the analysis of the brain dynamics involved in overriding emotional distraction, and all of them have limited their analysis to the particular connections between the amygdala and prefrontal cortex. In this study, we used magnetoencephalography (MEG) to characterize the mutual information–based functional connectivity dynamics among regions of interest located over the prefrontal, the parietal, the temporal, and the occipital cortex. Our results show that the detection of emotional distraction at early latencies (50–150 ms) induces a reduction of functional connectivity involving parietal and temporal cortices that are part of the frontoposterior WM network, while functional coupling among prefrontal areas and between them and posterior cortices is strengthened during the detection of emotional distractors. Later in the processing of the distractor (250–350 and 360–460 ms), the frontoposterior coupling is reestablished for a successful performance, while the orbitofrontal and ventrolateral prefrontal cortex become strongly connected to posterior cortices as a mechanism to cope with emotional distractors.

KEYWORDS
cognitive control, emotional interference, functional connectivity, prefrontal cortex, working memory

1 | INTRODUCTION

Active maintenance of information is the result of synchronized and sustained activity within local groups of neurons and over functional networks widely distributed across the brain (Fuster & Alexander, 1971; Goldman-Rakic, 1990; Miller, Erickson, & Desimone, 1996). Traditional approaches in neuroscience have demonstrated that several cortical regions across the frontoparietal cortex support working memory (WM) maintenance (Curtis & D'Esposito, 2003; Linden et al., 2003; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000; Todd & Marois, 2004) while occipital and temporal areas are related with the formation of sensory representation in visual WM (Desimone, 1998; Fuster, 1990; Miller & Desimone, 1994; Miller, Li, & Desimone, 1991; Miyashita, 2000; Ranganath, DeGutis, & D'Esposito, 2004). Moreover, investigations in the last decade have shown that sustained long-range functional coupling between frontal and posterior areas is a key mechanism for maintaining information in WM (Gazzaley, Rissman, & D'Esposito, 2004; Palva, Monto, Kulashekhar, & Palva, 2010; Rissman, Gazzaley, & D'Esposito, 2004, 2008; Sarnthein, 1998; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005). Since interference effects of irrelevant information in short-term memory have become an exciting field of research in cognitive psychology (see Jonides et al., 2008 for a review), there is also an increasing interest in how interfering information affects such frontoposterior network and how our cognitive system is able to override the influence of distraction in such dynamic functional interactions.

Several neuroimaging studies have explored the effect of distraction on the functional network that sustains WM by focusing in the prefrontal cortex and the posterior areas of the brain. Yoon, Curtis, and D'Esposito (2006) focused on the functional coupling of the dorsolateral prefrontal cortex (DLPFC) and the visual associative cortex during the delay period of a WM task with distraction. They showed that distractors with high similarity to the memorized material produced a disruption of the functional coupling between the DLPFC and the visual associative cortex, suggesting that the active maintenance of information is an emergent function of cooperative activity between the lateral prefrontal cortex (PFC) and the posterior sensory cortex. More interestingly, such a disruption of the frontoposterior functional connectivity has been shown to be restored after the presentation of the interfering stimuli (Clapp, Rubens, & Gazzaley, 2010). This result was interpreted as a mechanism responsible for the reactivation of the information previously encoded.

However, far too little attention has been paid to the effect of emotional distraction in the cortical functional networks that sustain WM maintenance. The interest on emotional interference arises from considering the privileged access of emotional stimulus to our focus of attention (Bradley et al., 2003; Lang et al., 1998; Morris, Ohman, & Dolan, 1998; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005). Because emotional stimuli are linked to our survival, they seem to automatically recruit attentional resources and might be difficult to ignore, even when task irrelevant. Emotional interference during WM performance thus offers a unique window into the interaction of hot and cold information in cognitive processing. The disruptive role of emotional distracting stimuli for WM seems well established, specifically for emotional distraction of negative valence (hereinafter, unpleasant distraction) (Anticevic, Repovs, & Barch, 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos, Diaz-Granados, Wang, & McCarthy, 2008; Dolcos & McCarthy, 2006; García-Pacios, Del Río, Villalobos, Ruiz-Vargas, & Maestú, 2015; García-Pacios, Garcés, Del Río, & Maestú, 2015). While the role of emotionally positive distraction (i.e., pleasant distraction) has been less studied, evidence suggests that it is similarly easy to ignore as nonemotional (i.e., neutral) distraction is (García-Pacios, Del Río, et al., 2015; García-Pacios, Garcés, et al., 2015). To the best of our knowledge, all previous studies addressing the effect of emotional distraction on brain functional connectivity have focused on frontolimbic connections while coping with emotionally negative distraction (Chuah et al., 2010; Dolcos, Kragel, Wang, & McCarthy, 2006). In accordance with previous literature, activity in the ventrolateral prefrontal cortex (VLPFC), the DLPFC, and the medial prefrontal cortex (MPFC) were shown to be highly coupled with activity in the amygdala during successful coping with emotional distraction. Finally, a recent fMRI study (Clarke & Johnstone, 2013) has assessed the effective connectivity pattern during the maintenance period of a WM task in which anxiety was induced by threat of an electric shock. Results of this study showed that the VLPFC and the anterior cingulate cortex exerted a top-down modulation of the amygdala and its output to the prefrontal cortex, inhibiting threat processing and enabling WM performance without threat-related interference.

In a recently published study by our group, we explored the temporal dynamics of the cognitive and brain mechanisms that allow people to cope with emotional distraction (García-Pacios, Garcés, et al., 2015). Using magnetoencephalography (MEG), we identified three time intervals of interest that appeared to be related to different mechanisms involved in the cognitive control of biologically relevant distractors. First, at a very early latency (70–130 ms following the onset of the distractor), prefrontal mechanisms were engaged for the rapid detection of both pleasant and unpleasant emotional distractors, according to previous literature that had linked those prefrontal effects to top-down facilitatory mechanisms in object recognition, in order to improve our preparation to adaptively respond to linked-to-survival stimuli (e.g., Bar, 2003; Kawabata et al., 2001). Later in the processing (360–455 ms), we identified activity enhancements over the DLPFC, the MPFC, and the orbitofrontal cortex (OFC) that were functionally related to the individual capacity to cope with unpleasant distractors. Finally, in the time between the early detection and the effective control of the emotional distraction, unpleasant distractors produced increased activity over the temporal lobe, probably reflecting the well-known episodic memory enhancement for emotional materials (Dolcos, Denkova, & Dolcos, 2012; Dolcos, Iordan, & Dolcos, 2011; Dolcos et al., 2013).

In the present study, we aim to evaluate functional connectivity during those previously characterized time intervals of interest in order to address the potential effect of emotional distraction in frontoposterior cortical networks during the active maintenance of information in WM. Based on existing literature showing an interference-based disruption of those functional connections (Clapp et al., 2010; Yoon et al., 2006), we expect that the frontoposterior network would be more disrupted by emotional distractors than by neutral ones, especially around 100 ms after the distractor presentation, when the detection of biologically relevant information takes place (Bar, 2003; Kawabata et al., 2001).

TABLE 1 Mean normative values of pictures and mean subjective ratings of those pictures by our volunteers. Standard deviations are shown in parentheses

Condition	IAPS valence	IAPS arousal	Subjective valence	Subjective arousal
Pleasant	7.42 (0.33)	6.16 (0.49)	7.30 (1.00)	6.33 (0.94)
Neutral	4.93 (0.35)	2.71 (0.38)	5.14 (0.49)	3.61 (1.33)
Unpleasant	2.48 (0.52)	6.16 (0.41)	2.42 (1.03)	6.77 (0.93)

Given the emotional nature of our distractors and according with the extensive literature that links the VLPFC to the successful coping with emotional distraction (Denkova et al., 2010; Dolcos et al., 2013, 2006; Dolcos & McCarthy, 2006; García-Pacios, Garcés, et al., 2015; Iordan, Dolcos, & Dolcos, 2013), we also hypothesize that at later latencies of the processing (250–500 ms) this prefrontal region would be highly functionally coupled with posterior areas as a mechanism to restrain the interfering effect of emotional stimuli on the maintenance of nonemotional information.

2 | METHOD

2.1 | Participants

The experimental sample consisted of 15 students from the Camilo José Cela University of Madrid (7 males and 8 females) with a mean age 20.06 years and a range between 18 and 29 years. All of them had normal or corrected-to-normal vision and completed the Spanish version of the Spielberger State-Trait Anxiety Inventory for Adults (Spielberger, Gorsuch, & Lushene, 2002) (mean State score 15.07, *SD*: 7.17; mean Trait score 12.36, *SD*: 5.88) and the Beck Depression Inventory (Beck, Steer, & Brown, 2006) (mean score 6.46, *SD*: 5.10). Volunteers received course credits for their time. The project was approved by the institutional review committee of the Center for Biomedical Technology (Technical University of Madrid and Complutense University of Madrid) as well as for the research ethical committee of the Camilo José Cela University.

2.2 | Materials

Items at encoding and recognition stages consisted of colored images of neutral faces. An oval mask was applied along the contours of the faces to remove any potential non-face-specific cues. Faces were assigned to different experimental conditions across participants. For the interfering items presented at the maintenance period, the International Affective Picture System (IAPS) (Lang, Bradley, & Cuthbert, 2005) was scanned to obtain three sets of pictures matched in luminance, contrast, color, and figure-ground relationships that formed the unpleasant distractors (e.g., scenes of aggressive behavior, mutilations, etc.), pleasant (e.g., pictures depicting familiar interactions, adventure sports, erotic scenes, etc.), and neutral (e.g., mundane activities). Pictures in the pleasant and unpleasant distraction conditions were selected to differ in valence but not in arousal. Forty-eight pictures between 8.5–6.5 valence and 7.5–5.5 arousal formed the pleasant condition. Another 48 pictures between 3.5–1.4 valence and 6.6–4.3 arousal formed the unpleasant condition. Finally, 48 medium-valenced (5.5–4.0) and low-arousing (3.7–1.7) pictures were selected for the neutral distraction condition (see Table 1 for mean normative values).

2.3 | Procedure

A delayed-recognition WM paradigm with three experimental conditions—pleasant, neutral, and unpleasant interference—was used (Figure 1). Each trial began with a 1,000 ms intertrial interval (ITI), followed by the presentation of a pair of faces for 2,000 ms (encoding phase). After a 1,000 ms blank screen, an interfering stimulus was presented for 2,000 ms, followed by another 1,000 ms blank screen (maintenance phase). Next, just one face appeared on the screen for 1,500 ms, followed by a 500 ms blank screen (recognition stage). Participants had to decide whether the face at the recognition stage had been one of the two previously encoded or not, by pressing one of two buttons.

In order to achieve an adequate signal-to-noise ratio for subsequent brain source estimation, each experimental condition consisted of 96 trials. Therefore, each one of the 48 previously selected interfering pictures was employed in two different trials. The order of trials was constrained so that no more than three trials of the same condition were consecutively presented in order to avoid inducing long-lasting mood states. To prevent any potential habituation effect, the two presentations of the same interfering picture were separated by a minimum of 30 trials. Once the WM paradigm was completed, participants were asked to rate the emotional valence and arousal in all the pictures used as interference, using the Self-Assessment Manikin (SAM) self-report scale (Lang, 1980) in order to confirm that they perceived them as expected (see García-Pacios, Garcés, et al., 2015 for a detailed description of the procedure).

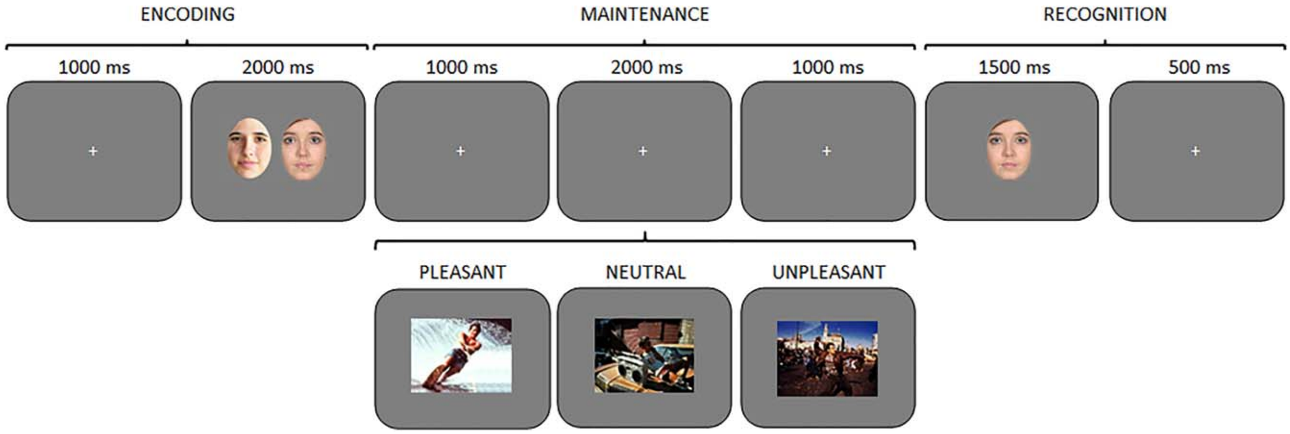

FIGURE 1 A representative trial of the delayed-recognition WM paradigm. Pleasant, neutral, and unpleasant distractors were pseudo-randomly presented during the maintenance stage. Volunteers were trained to learn and maintain the pair of faces into WM, look at the distracter, and then indicate by pressing one of two keys whether the face at the recognition stage was one of the two previously encoded or not

2.3.1 | Data acquisition and preprocessing

MEG data were measured for each participant during the performance of the WM task using an Elekta© Vectorview system with 306 channels (102 magnetometers and 204 planar gradiometers) placed inside a magnetically shielded room (Vacuumschmelze GmbH, Hanau, Germany). Recordings were sampled at 1000 Hz with a 0.01–330 Hz online filter, and EOG electrodes were placed above and below the eye to control for ocular movements. External noise in the MEG recordings was removed with the spatiotemporal signal space separation method (Taulu & Simola, 2006), as implemented in the Maxfilter software (version 2.2., Elekta Neuromag).

Raw data were then processed with MATLAB© by combining in-house code and functions from the FieldTrip toolbox (http://fieldtrip.fcdonders.nl/). MEG data were first band pass filtered in the 1–45 Hz range and segmented into 2,300 ms trials, which spanned from −300 ms to +2,000 ms relative to the distractor onset. The 300 ms interval prior to the distractor onset was then employed for baseline correction and was subtracted to each trial and channel. Trials with incorrect responses were not taken into account in the analysis (average errors for pleasant: 18.80, *SD*: 5.00; neutral: 19.40, *SD*: 4.47; and unpleasant condition: 21.60, *SD*: 3.89). The remaining trials were then visually scanned for artifacts, and all trials containing either ocular, muscular, or movement artifacts, or amplitudes higher than 3 pT, were discarded from the analysis (average artefacts for pleasant: 11.33, *SD*: 5.15; neutral: 12.00, *SD*: 7.54; and unpleasant condition: 12.67, *SD*: 4.79). Finally, the amount of clean trials included in the analysis was matched among conditions to prevent biases in further analyses (average: 60.20, *SD*: 4.87). A minimum of 52 trials were included for each participant and condition. Only magnetometer data were employed for further source reconstruction. We note, however, that the preprocessed magnetometer data results from a signal space separation, which estimates inside components with the raw 102 magnetometers and 204 gradiometers (Taulu & Kajola, 2005).

2.3.2 | Source reconstruction

Source activity was reconstructed around three time intervals of interest which were previously proven to be relevant in the cognitive control of emotional distraction using the present WM task (García-Pacios, Garcés, et al., 2015): 70–130 ms, 280–320 ms, and 360–455 ms. As we used Mutual Information (MI) as our estimate of functional brain connectivity (see below) and longer time series generate more robust entropy and MI estimates (Knuth, 2006), temporal windows were enlarged to 100 ms, so that the final temporal windows of interest for source reconstruction and further functional connectivity analysis were 50–150 ms, 250–350 ms, and 360–460 ms.

Two thousand four hundred seventy-one source positions were defined in Montreal Neurological Institute (MNI) space and located in a regular three-dimensional grid with 1-cm spacing. They were then transformed into participant's space with a homogeneous transformation that was obtained by matching the participant's head shape and a standard MNI skin with an iterative closest point algorithm. The forward problem was then solved with a local spheres method, as introduced in Huang, Mosher, and Leahy (1999). Source time series were then computed with a linearly constrained minimum variance beamformer (Van Veen, 1997). For each participant, temporal window, and source location, a single beamforming filter was computed, using the average covariance matrix over all three conditions for this temporal window. This filter was then applied to the individual trials of all three conditions to extract the activity time series for all individual trials.

2.3.3 | Functional connectivity

Functional connectivity was computed between each pair of cortical regions (41 per hemisphere) in the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer & Landeau, 2002), as implemented in the Wake Forest University (WFU) software (Maldjian, Laurienti, Kraft, & Burdette, 2003). Next, the correlation between all sources belonging to the same cortical region was computed using all trials (across all three conditions), and the source with highest average correlation with the remaining sources was selected. The time series of this source was selected as the representative time series for this cortical region, as proposed by Hillebrand, Barnes, Bosboom, Berendse, and Stam (2012). Then, functional connectivity between each pair of regions and trial was computed, using MI. MI assesses the relationship between two time series using Shannon Entropy (Shannon, 1948) and Information Theory (Pereda, Quiroga, & Bhattacharya, 2005), capturing both linear and nonlinear interactions. It quantifies the amount of information that is shared between two source time series. Prior to MI computation, a time-domain leakage correction was performed as indicated in Brookes, Woolrich, and Barnes (2012). For each pair of regions i and j, source time series x_i and x_j were orthogonalized following:

$$x_{j,orth} = x_j - b_{ji} \cdot x_i$$

where b_{ij} is the regression coefficient between x_i and x_j. MI values were averaged over trials, yielding an 82 x 82 connectivity matrix per participant, condition, and time window of interest.

2.3.4 | Statistical analysis

In order to robustly compare functional connectivity between conditions while limiting the number of comparisons, we focused on 14 broader regions of interest (ROIs) rather than the 82 AAL regions. These ROIs were selected to comprise both anterior and posterior cortical regions previously reported as involved in the effective control of emotional distraction (García-Pacios, Garcés, et al., 2015; see also Iordan et al., 2013 for a comprehensive review of neural correlates of the response to emotional distraction in WM) (see Table 2 for correspondence between these 14 ROIs and the AAL regions). For each pair of non-neighboring ROIs and temporal window, the statistical difference between conditions was tested with the following linear mixed-effects model (Pinheiro & Bates, 1996): Functional Connectivity $\sim 1 + \text{condition} + (1|\text{participant}) + (1|\text{AALlink})$, where "AALlink" is a categorical variable denoting a given pair of regions of the AAL atlas (note that the ROIs employed here contain several AAL regions, and therefore a connection between two ROIs comprises several connections between AAL regions). To correct for the multiple comparisons in this study: 3 temporal windows x 62 connections (between 14 ROIs) x 3 condition contrasts, a single False discovery rate (FDR) (Benjamini & Yekutieli, 2001) was employed.

3 | RESULTS

3.1 | Working memory performance

Friedman's test showed a significant main effect of condition in WM performance (hits + correct rejections) [$\chi^2(3) = 12.21$, $p = .001$)]. Wilcoxon's test for pairwise comparisons revealed that performance after unpleasant distraction (77.5%) was lower than after pleasant (80.41%) ($p < .01$) and neutral (79.79%) ($p < .05$) distraction. Neutral and pleasant distraction did not differ in performance ($p > .1$). These differences in WM performance were confirmed when corrected recognition scores (hits rate – false alarms rate) were used as dependent variables [$\chi^2(3) = 8.13$, $p = .01$); pleasant > unpleasant ($p = .01$); neutral > unpleasant ($p < .005$); pleasant = neutral ($p > .1$)] (see García-Pacios, Garcés, et al., 2015 for a more detailed description of the WM performance).

3.2 | Subjective emotional ratings

As expected, Friedman's test showed a significant main effect of affective category in subjective valence ratings [$\chi^2(2) = 30.00$, $p < .001$)]. Pleasant distractors were rated as the most pleasant followed by neutral distractors. Volunteers rated unpleasant distractors as the least pleasant (mean valence ratings: 7.14, *SD*: 0.52 [pleasant], 5.09, *SD*: 0.52 [neutral], 2.23, *SD*: 0.82 [unpleasant], $p = .001$ for all comparisons). Arousal ratings also differed as a function of affective category [$\chi^2(2) = 25.20$, $p < .001$)], with pleasant and unpleasant distractors perceived as more arousing than neutral distractors (mean arousal ratings: 5.35, *SD*: 1.20 [pleasant], 2.27, *SD*: 0.5 [neutral], 6.48, *SD*: 0.48 [unpleasant], $p = .001$ for both comparisons). Volunteers rated unpleasant distractors as more arousing than pleasant distractors ($p < .01$) (see Table 1 for mean subjective values).

3.3 | Brain connectivity

MI strength values were compared across conditions (neutral, unpleasant, and pleasant distractions) for each time window and connection between two ROIs (or link). The statistical results are described in the following for each time window separately.

3.3.1 | First temporal window of interest, 50–150 ms

Functional connectivity involving prefrontal areas was higher for emotional than for neutral distraction during the first

TABLE 2 List of ROIs and their corresponding AAL regions. These 7 ROIs were employed for each hemisphere, thus yielding 14 ROIs in total

ROI acronym	ROI name	Corresponding AAL regions
DLPFC	Dorsolateral prefrontal cortex	Superior frontal gyrus, middle frontal gyrus
VLPFC	Ventrolateral prefrontal cortex	Triangular and opercular parts of the inferior frontal gyrus, insula
OFC	Orbital frontal cortex	Orbital parts of superior, middle and inferior frontal gyri, gyrus rectus
MPFC	Medial prefrontal cortex	Medial superior frontal gyrus, anterior and median cingulate and paracingulate gyri
OC	Occipital cortex	Inferior and middle occipital gyri
TC	Temporal cortex	Superior, middle and inferior temporal gyri, Heschl gyrus
PC	Parietal cortex	Postcentral gyrus, precuneus, inferior parietal gyrus

temporal window of interest, between 50 and 150 ms. Specifically, functional coupling between bilateral DLPFC and between right DLPFC and left MPFC was higher in unpleasant than in neutral distraction. Functional connectivity between left OFC and temporal cortex (TC) and occipital cortex (OC) was also higher for pleasant than for neutral distraction. Interestingly, links involving parietal cortex (PC) showed lower values of functional connectivity during both unpleasant and pleasant than during neutral distraction. Finally, bilateral MPFC was more coupled with TC in unpleasant than in pleasant distraction, while bilateral OFC and right VLPFC were more coupled with TC in pleasant than in unpleasant distraction. (See Figure 2 and Table 3 for specific functional connections between cortical areas and associated *p* values. See also supplementary material for ROI x ROI connectivity matrices and ROI x ROI connectivity differences between conditions.)

3.3.2 | Second temporal window of interest, 250–350 ms

Emotional distraction significantly increased the level of connectivity between prefrontal cortex and posterior as well as temporal cortex, between 250 and 350 ms. Specifically, bilateral MPFC and DLPFC, VLPFC, and OFC of the right hemisphere were more functionally coupled with left TC for unpleasant than for neutral distraction. Also, functional connectivity between OFC and PC of the right hemisphere, and between left MPFC and right OC was higher during unpleasant than during neutral distraction. In a similar way, all prefrontal areas of the right hemisphere, including DLPFC, VLPFC, OFC, and MPFC were more functionally coupled with bilateral TC during pleasant than during neutral distraction. DLPFC and PC of the right hemisphere showed also higher values of functional connectivity during pleasant

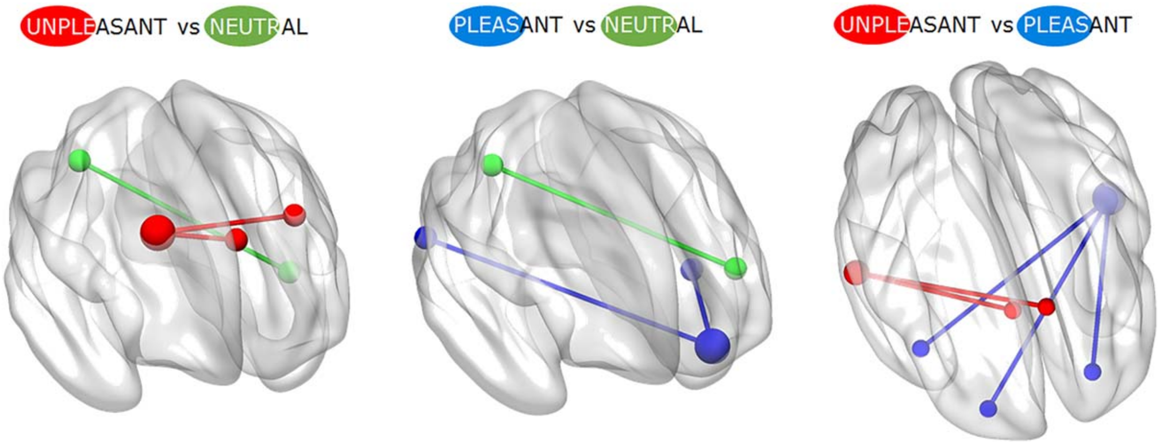

FIGURE 2 Statistical differences in functional brain connectivity at 50–150 ms, false discovery rate corrected, $q = 0.05$. Functional connectivity involving parietal cortices was higher in neutral distraction than in both pleasant and unpleasant distraction. Besides, functional coupling involving prefrontal regions was higher for both pleasant and unpleasant than for neutral distraction. Links in green represent significant higher connectivity for neutral distraction; links in red represent significant higher connectivity for unpleasant distraction; and links in blue represent significant higher connectivity for pleasant distraction

TABLE 3 Significant connections, false discovery rate corrected, $q = 0.05$, between cortical regions. A total of 14 cortical regions (7 regions per hemisphere) were included in the analysis. R: right hemisphere; L: left hemisphere; DLPFC: dorsolateral prefrontal cortex; VLPFC: ventrolateral prefrontal cortex; OFC: orbitofrontal cortex; MPFC: medial prefrontal cortex; OC: occipital cortex; TC: temporal cortex; PC: parietal cortex. The average MI value (and standard deviation in parentheses) for condition, and the adjusted p value using the FDR procedure ($q = 0.05$) are showed for each significant connection

50–150 ms

UNPLEASANT > NEUTRAL	**Unpleasant MI value**	**Neutral MI value**	***p* value**	**UNPLEASANT < NEUTRAL**	**Unpleasant MI value**	**Neutral MI value**	***p* value**
DLPFC.L – DLPFC.R	0.304 (0.003)	0.300 (0.004)	0.018	TC.L – PC.R	0.314 (0.005)	0.316 (0.005)	0.004
MPFC.L – DLPFC.R	0.304 (0.002)	0.301 (0.003)	0.012				

PLEASANT > NEUTRAL	**Pleasant MI value**	**Neutral MI value**	***p* value**	**PLEASANT < NEUTRAL**	**Pleasant MI value**	**Neutral MI value**	***p* value**
OFC.L – TC.L	0.314 (0.005)	0.312 (0.005)	0.035	VLPFC.L – PC.R	0.309 (0.005)	0.311 (0.006)	0.026
OFC.L – OC.R	0.315 (0.004)	0.312 (0.004)	0.007				

UNPLEASANT > PLEASANT	**Unpleasant MI value**	**Pleasant MI value**	***p* value**	**UNPLEASANT < PLEASANT**	**Unpleasant MI value**	**Pleasant MI value**	***p* value**
MPFC.L – TC.R	0.313 (0.004)	0.311 (0.005)	0.006	VLPFC.R – TC.L	0.312 (0.004)	0.314 (0.005)	0.045
MPFC.R – TC.R	0.312 (0.003)	0.310 (0.005)	0.026	OFC.L – TC.L	0.312 (0.005)	0.314 (0.005)	0.000
				OFC.R – TC.L	0.311 (0.004)	0.313 (0.005)	0.026

250–350 ms

UNPLEASANT > NEUTRAL	**Unpleasant MI value**	**Neutral MI value**	***p* value**	**UNPLEASANT < NEUTRAL**	**Unpleasant MI value**	**Neutral MI value**	***p* value**
VLPFC.L – DLPFC.R	0.308 (0.006)	0.305 (0.005)	0.001				
VLPFC.L – VLPFC.R	0.312 (0.005)	0.308 (0.006)	0.000				
VLPFC.L – MPFC.L	0.311 (0.005)	0.308 (0.005)	0.006				
VLPFC.L – MPFC.R	0.310 (0.005)	0.307 (0.005)	0.000				
VLPFC.L – OFC.R	0.311 (0.005)	0.308 (0.006)	0.000				
VLPFC.R – MPFC.R	0.310 (0.005)	0.306 (0.003)	0.000				
OFC.L – DLPFC.R	0.307 (0.005)	0.304 (0.004)	0.000				
OFC.L – VLPFC.R	0.311 (0.005)	0.308 (0.005)	0.000				
MPFC.L – DLPFC.R	0.306 (0.004)	0.303 (0.004)	0.019				
MPFC.L – VLPFC.R	0.310 (0.005)	0.307 (0.005)	0.002				
MPFC.L – TC.L	0.313 (0.005)	0.311 (0.006)	0.016				
MPFC.L – OC.R	0.313 (0.005)	0.310 (0.005)	0.026				
DLPFC.R – TC.L	0.312 (0.006)	0.308 (0.006)	0.000				

(Continues)

TABLE 3 (Continued)

250–350 ms						
UNPLEASANT > NEUTRAL				**UNPLEASANT < NEUTRAL**		
	Unpleasant MI value	**Neutral MI value**	***p* value**	**Unpleasant MI value**	**Neutral MI value**	***p* value**
VLPFC.R – TC.L	0.316 (0.007)	0.312 (0.006)	0.000			
OFC.R – TC.L	0.313 (0.006)	0.311 (0.005)	0.000			
OFC.R – PC.R	0.311 (0.004)	0.309 (0.004)	0.026			
MPFC.R – TC.L	0.313 (0.006)	0.310 (0.005)	0.000			
TC.L – OC.R	0.318 (0.006)	0.315 (0. 004)	0.028			
PLEASANT > NEUTRAL				**PLEASANT < NEUTRAL**		
	Pleasant MI value	**Neutral MI value**	***p* value**	**Pleasant MI value**	**Neutral MI value**	***p* value**
VLPFC.R – MPFC.R	0.308 (0.004)	0.306 (0.003)	0.003			
VLPFC.R – TC.L	0.314 (0.005)	0.312 (0.006)	0.029			
DLPFC.R – TC.R	0.311 (0.005)	0.308 (0.003)	0.029			
DLPFC.R – PC.R	0.309 (0.005)	0.306 (0.005)	0.003			
MPFC.R – TC.R	0.313 (0.006)	0.310 (0.004)	0.000			
OFC.R – TC.L	0.314 (0.005)	0.311 (0.005)	0.000			
OC.L – TC.R	0.320 (0.007)	0.317 (0.006)	0.043			
TC.L – OC.R	0.318 (0.005)	0.315 (0.004)	0.026			
UNPLEASANT > PLEASANT				**UNPLEASANT < PLEASANT**		
	Unpleasant MI value	**Pleasant MI value**	***p* value**	**Unpleasant MI value**	**Pleasant MI value**	***p* value**
VLPFC.L – MPFC.L	0.311 (0.005)	0.307 (0.006)	0.000			
VLPFC.L – VLPFC.R	0.312 (0.005)	0.309 (0.005)	0.008			
VLPFC.L – OFC.R	0.311 (0.005)	0.308 (0.005)	0.000			
VLPFC.L – MPFC.R	0.310 (0.005)	0.307 (0.005)	0.001			
OFC.L – DLPFC.R	0.307 (0.005)	0.304 (0.003)	0.008			
360–460 ms						
UNPLEASANT > NEUTRAL				**UNPLEASANT < NEUTRAL**		
	Unpleasant MI value	**Neutral MI value**	**p value**	**Unpleasant MI value**	**Neutral MI value**	**p value**
VLPFC.L – OC.L	0.315 (0.006)	0.312 (0.006)	0.044			
VLPFC.L – OC.R	0.313 (0.005)	0.309 (0.006)	0.000			
VLPFC.L – TC.R	0.315 (0.007)	0.312 (0.006)	0.000			
VLPFC.R – OC.R	0.314 (0.006)	0.311 (0.006)	0.044			

(Continues)

TABLE 3 (Continued)

360–460 ms							
UNPLEASANT > NEUTRAL				**UNPLEASANT < NEUTRAL**			
	Unpleasant MI value	**Neutral MI value**	**p value**		**Unpleasant MI value**	**Neutral MI value**	**p value**
OFC.R – TC.R	0.313 (0.005)	0.312 (0.006)	0.004				
OFC.R – PC.L	0.311 (0.005)	0.309 (0.005)	0.024				
TC.L – OC.R	0.317 (0.006)	0.314 (0.006)	0.026				
PC.L – TC.R	0.316 (0.007)	0.314 (0.005)	0.008				
PLEASANT > NEUTRAL				**PLEASANT < NEUTRAL**			
	Pleasant MI value	**Neutral MI value**	***p* value**		**Pleasant MI value**	**Neutral MI value**	***p* value**
VLPFC.L – TC.R	0.314 (0.006)	0.312 (0.006)	0.013	DLPFC.L – MPFC.R	0.303 (0.004)	0.306 (0.004)	0.024
UNPLEASANT > PLEASANT				**UNPLEASANT < PLEASANT**			
	Unpleasant MI value	**Pleasant MI value**	***p* value**		**Unpleasant MI value**	**Pleasant MI value**	***p* value**
VLPFC.L – OC.R	0.313 (0.005)	0.311 (0.007)	0.024				
VLPFC.R – OC.R	0.314 (0.006)	0.311 (0.005)	0.026				
OFC.L – TC.R	0.314 (0.005)	0.313 (0.005)	0.032				
OFC.L – PC.R	0.311 (0.005)	0.309 (0.004)	0.017				

distraction in this same contrast. Interestingly, increased interhemispheric functional connectivity among prefrontal areas was evident for unpleasant distraction when compared with both neutral and pleasant distraction, in particular for those links involving left VLPFC and OFC, while VLPFC and MPFC of the right hemisphere were more coupled during both unpleasant and pleasant distraction than for neutral distraction. Finally, posterior interhemispheric connections, including OC and TC, were enhanced during both emotional distraction conditions than for neutral distraction. (See Figure 3 and Table 3

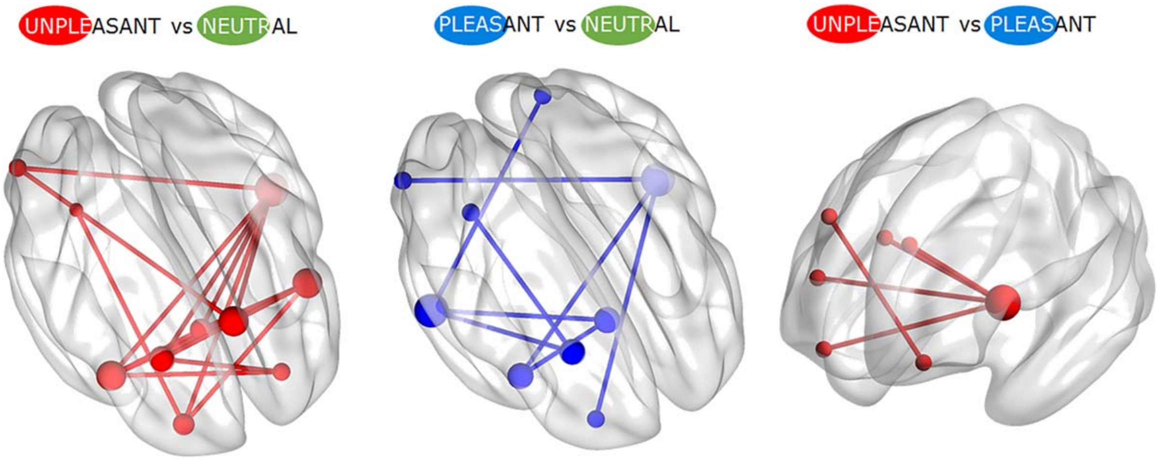

FIGURE 3 Statistical differences in functional brain connectivity at 250–350 ms, false discovery rate corrected, $q = 0.05$. Functional connectivity between prefrontal cortex and posterior and temporal cortex was higher in both pleasant and unpleasant than in neutral distraction. Functional coupling among prefrontal areas was also higher in unpleasant than in both neutral and pleasant distraction. Links in green represent significant higher connectivity for neutral distraction; links in red represent significant higher connectivity for unpleasant distraction; and links in blue represent significant higher connectivity for pleasant distraction

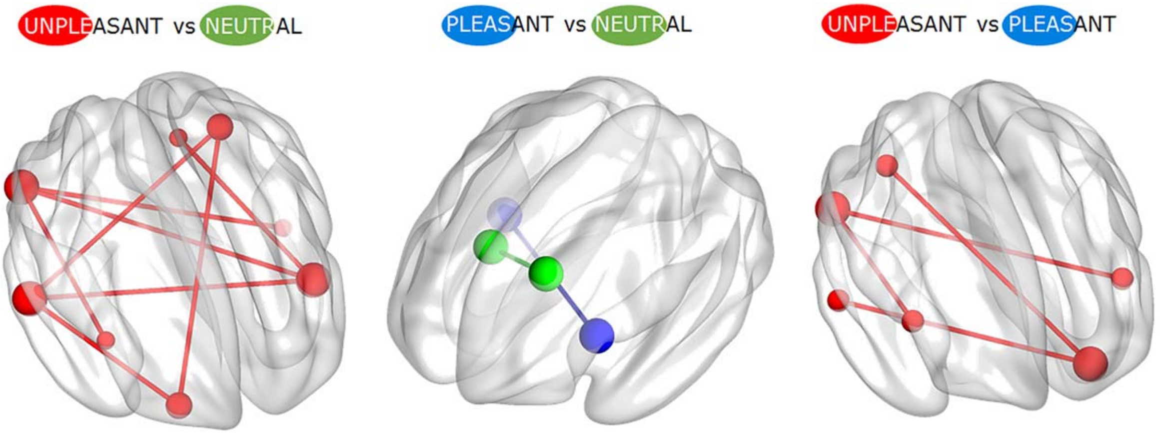

FIGURE 4 Statistical differences in functional brain connectivity at 360–460 ms, false discovery rate corrected, $q = 0.05$. Unpleasant distraction enhanced functional connectivity between VLPFC and OFC, and TC, OC, and PC when compared with both neutral and pleasant distraction. Functional interhemispheric coupling between left VLPFC and right TC was also higher in pleasant than in neutral distraction. Links in green represent significant higher connectivity for neutral distraction; links in red represent significant higher connectivity for unpleasant distraction; and links in blue represent significant higher connectivity for pleasant distraction

for specific functional connections between cortical areas and associated *p* values. See also supplementary material for ROI x ROI connectivity matrices and ROI x ROI connectivity differences between conditions.)

3.3.3 | Third temporal window of interest, 360–460 ms

Unpleasant distraction significantly increased the level of connectivity between VLPFC and OFC, and TC, OC, and PC when compared with both neutral and pleasant distraction, between 360 and 460 ms. Bilateral VLPFC and right OFC were more coupled with PC, OC, and TC, and the latter among them during unpleasant than during neutral condition. Unpleasant distraction also enhanced functional connectivity between bilateral VLPFC and right OC, as well as between left OFC and right TC and PC. Finally, functional connectivity between left VLPFC and right TC was higher for pleasant than for neutral distraction, and the reverse was true for connection between left DLPFC and right MPFC. (See Figure 4 and Table 3 for specific functional connections between cortical areas and associated *p* values. See also supplementary material for ROI x ROI connectivity matrices and ROI x ROI connectivity differences between conditions.)

4 | DISCUSSION

Previous research employing different neuroimaging modalities such as fMRI or electrophysiological recordings (both EEG and MEG) have agreed in showing that long-range functional coupling between frontal and posterior areas plays an important role in maintaining information in WM (Gazzaley et al., 2004; Palva et al., 2010; Rissman et al., 2004, 2008; Sarnthein, 1998; Sauseng et al., 2005). Additionally, recent fMRI studies have demonstrated that interfering information can impair WM retention by disrupting the functional coupling between the PC and the PC and other posterior areas (Clapp et al., 2010; Yoon et al., 2006). However, the specific effect of emotional distraction in such a frontoposterior network has not been explored yet, although the VLPFC is thought to be crucial as it has been reported active in coping with emotional distraction (Denkova et al., 2010; Dolcos et al., 2013, 2006; Dolcos & McCarthy, 2006; García-Pacios, Garcés, et al., 2015; Iordan et al., 2013), and functionally coupled with amygdala while overriding these kind of distractors (Chuah et al., 2010; Dolcos et al., 2006).

Based on results obtained in a previous analysis of event-related activity from this same data set (García-Pacios, Garcés, et al., 2015), we focused on three time windows of interest in which differences between emotional and neutral distraction arose at the brain activity level. During the earliest temporal window of interest, between 50 and 150 ms, both types of emotional distractors seemed to alter functional connectivity involving parietal and temporal cortices, when compared with neutral distraction. The parietotemporal cortex is part of the frontoposterior network widely related with WM maintenance (Gazzaley et al., 2004; Palva et al., 2010; Rissman et al., 2004, 2008; Sarnthein, 1998; Sauseng et al., 2005), and it has been consistently reported to be active during retention of information in WM (e.g., Corbetta, Kincade, & Shulman, 2002; Courtney, Ungerleider, Keil, & Haxby, 1997; Curtis & D'Esposito, 2003; Miyashita, 2000; Ranganath et al., 2004; Todd & Marois, 2004). Moreover, cortical regions surrounding the intraparietal sulcus are considered a primary area in the network that sustains WM (Palva et al., 2010). Therefore, the observed functional connectivity reduction of links involving this component of the frontoposterior network, in comparison with neutral distraction, may be reflecting the attentional capture of emotional distractors disrupting the maintenance of task-relevant information in WM. This interpretation is consistent with previous findings of disrupted functional connectivity in WM at the time an interfering stimulus is encountered (Clapp et al., 2010; Yoon et al., 2006). At the same time, emotional distraction increased functional coupling among prefrontal regions, including MPFC and DLPFC, as well as between prefrontal regions, including MPFC, OFC, and VLPFC, and posterior areas such as TC and OC. The MPFC is known to be involved in assessing the salience of emotional information (see Bush, Luu, & Posner, 2000 for a review) as well as in allocating attentional resources (Small et al., 2003). The DLPFC, among other prefrontal regions, has been reported active during visual recognition at early latencies of such a process (Barbas, 1995; Funahashi, Bruce, & Goldman-Rakic, 1990; García-Pacios, Garcés, et al., 2015; Paradiso et al., 1999), and in combination with OFC and VLPFC they have been proposed as part of a top-down visual processing mechanism that would be highly adaptive in the fast detection of biologically relevant information (Bar, 2003; see also García-Pacios, Garcés, et al., 2015). According to Bar's (2003) model, it is conceivable that the detection of emotional distraction increases functional coupling among prefrontal regions, including MPFC, and between them and posterior cortices, in a mechanism that facilitates the rapid identification of biologically relevant information, as such contained in emotional distractors (García-Pacios, Garcés, et al., 2015).

However, a sustained disruption of functional connectivity involving parietotemporal components of the frontoposterior network responsible of WM maintenance might lead to the interruption of the information maintenance, and may finally produce the forgetting of the initially encoded materials (Clapp, Rubens, Sabharwal, & Gazzaley, 2011). In accordance with previous studies showing that the functional frontoposterior coupling is reactivated after the presentation of an interfering stimuli (Clapp et al., 2010, 2011), functional coupling involving parietotemporal areas returned to levels observed during neutral distraction, in the second temporal window of interest, about 250–350 ms. More interestingly, both types of emotional distraction increased functional coupling between the prefrontal cortex and posterior cortices including TC, PC, and OC. Specifically, right VLPFC-OFC and parietotemporal cortices showed greater values of functional connectivity during unpleasant and pleasant distraction than during neutral distraction. As commented above, although cortico-cortical connectivity while coping with emotional distraction in WM has not been previously addressed, the VLPFC is highly coupled with the amygdala and modulates projections from this nucleus to the prefrontal cortex while facing with emotional distractors (Chuah et al., 2010; Clarke & Johnstone, 2013; Dolcos et al., 2006). Moreover, the VLPFC is considered a crucial cortical region in the successful cognitive control of emotional distraction (Anticevic et al., 2010; Denkova et al., 2010; Dolcos et al., 2013; Dolcos & McCarthy, 2006; García-Pacios, Garcés, et al., 2015). Therefore, we suggest that this specific frontoposterior coupling might sustain specific control mechanisms of the emotional distractor. Additionally, DLPFC and MPFC, which have been largely related to successful performance in WM and cognitive control tasks (D'Esposito, Postle, & Rypma, 2000; Nee et al., 2013; Smith & Jonides, 1999), also revealed greater values of functional connectivity with posterior areas during both emotional distractions than during neutral distraction. Indeed, DLPFC and MPFC have been reported as important areas for interference resolution (Jha, Fabian, & Aguirre, 2004; Menon, Adleman, White, Glover, & Reiss, 2001; Nee, Wager, & Jonides, 2007). According to this rationale, these prefrontal areas not only showed enhanced connectivity with posterior areas during both emotional distractions but also among them and between hemispheres, probably due to the greater engagement of executive resources for a successful performance. Interesting enough, this pattern of enhanced coupling among prefrontal areas appeared more evident for unpleasant than for pleasant distraction, when both compared with neutral distraction, as well as when one compared to each other. This particular result is consistent with behavioral performance and with a previous study by our group (García-Pacios, Garcés, et al., 2015), as unpleasant distractors seemed to be more difficult to cope with than neutral and pleasant distractors (García-Pacios, Del Río, et al., 2015; García-Pacios, Garcés, et al., 2015).

During the last temporal window of interest, between 360 and 460 ms after the onset of the distractor, unpleasant distraction increased connectivity values between both VLPFC and OFC, and posterior areas including PC, TC, and OC links in comparison with both neutral and pleasant distraction. As previously discussed, VLPFC is known to be critically engaged in coping with emotional distraction (Iordan et al., 2013). Besides, fMRI, EEG, and lesion studies have demonstrated that the OFC is highly implicated in the inhibition of prepotent responses (Bokura, Yamaguchi, & Kobayashi, 2001; Casey et al., 1997; Jones & Mishkin, 1972; Kowalska, Bachevalier, & Mishkin, 1991; Malloy, Bihrle, Duffy, & Cimino, 1993; Perret, 1974), especially when such responses were established upon their previous reward value (Iversen & Mishkin, 1970). Because the attentional capture elicited by unpleasant stimuli, which are potentially threatening, may be considered a prepotent attentional response that should be overridden in our task for a successful WM performance, it is conceivable that OFC appeared strongly linked with posterior areas when a powerful distractor is encountered (García-Pacios, Garcés, et al., 2015).

The present study constitutes the first approximation to the temporal dynamics of the functional interactions implicated in the maintenance of information in WM, while coping with emotional distraction. Consistent with previous literature in the study of the cognitive control of distraction in WM, our results showed that emotional stimuli alter functional connectivity involving parietal and temporal cortices, which are important components of the well-known fronto-posterior network that is supposed to sustain the WM maintenance (Clapp et al., 2010, 2011; Palva et al., 2010; Yoon et al., 2006). Our results also confirmed that functional connectivity involving these regions can be reestablished for a successful behavioral performance (Clapp et al., 2010, 2011), extending previous findings from nonemotional distraction to the emotional domain. Interesting enough, functional connectivity among prefrontal regions, including MPFC, DLPFC, and OFC, and between them and posterior cortices is strengthened during the early detection of emotional distractors (Bar, 2003; García-Pacios, Garcés, et al., 2015). At medium latencies, the enhancement of functional connectivity between the VLPFC-OFC and posterior regions probably reflects control mechanisms of the emotional distractor, which become more evident for unpleasant distractors as they contain potentially threatening information, which make them more difficult to cope with (Anticevic et al., 2010; Chuah et al., 2010; Denkova et al., 2010; Dolcos et al., 2008; Dolcos & McCarthy, 2006; García-Pacios, Del Río, et al., 2015; García-Pacios, Garcés, et al., 2015).

Despite of the accordance of the present findings with previous research, whole-brain functional connectivity estimation with MEG still has limitations that should be taken into account when considering these results. Mainly, the spatial resolution in the source reconstruction (and functional connectivity estimation) is limited both by the ill-posed inverse problem and by the fact that the spatiotemporal signal space separation method implemented in the Maxfilter software usually considers less independent components that original regions in the anatomical atlas here employed (Taulu & Simola, 2006). On the other hand, MRIs were not available for the participants to generate head models, which would have accurately followed the participants' cortical and brain surfaces. Finally, the relative small size of the sample, as well as the fact that they were relatively young and highly educated, might limit the representativeness of the sample.

Nevertheless, it is remarkable that these findings are in close accordance with results from a previous event-related fields study using this same data set, recently published by our group (García-Pacios, Garcés, et al., 2015). Results from that study also showed that prefrontal cortices, particularly DLPFC, VLPFC, OFC, and MPFC, were recruited at very early latencies for the rapid detection of emotional distraction. Later in the processing, OFC and VLPFC were involved in the effective control of the emotional distraction. The functional connectivity approach presented here add valuable insights into how these brain regions interact among them and with posterior cortices to achieve a successful WM performance even in the presence of biologically relevant distractors. The present findings highlight the temporal dynamics of functional interactions that sustains our ability to cope with emotional distraction, while providing evidence for differential mechanisms implicated in the maintenance of information in WM and in the effective control of emotional distractors.

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Supplementary Figures

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