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Neural networks supporting autobiographical memory retrieval in posttraumatic stress disorder

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Abstract Posttraumatic stress disorder (PTSD) affects the functional recruitment and connectivity between neural regions during autobiographical memory (AM) retrieval that overlap with default and control networks. Whether such univariate changes relate to potential differences in the contributions of the large-scale neural networks supporting cognition in PTSD is unknown. In the present functional MRI study, we employed independent-component analysis to examine the influence of the engagement of neural networks during the recall of personal memories in a PTSD group (15 participants) as compared to non-trauma-exposed healthy controls (14 participants). We found that the PTSD group recruited similar neural networks when compared to the controls during AM recall, including default-network subsystems and control networks, but group differences emerged in the spatial and temporal characteristics of these networks. First, we found spatial differences in the contributions of the anterior and posterior midline across the networks, and of the amygdala in particular, for the medial temporal subsystem of the default network. Second, we found temporal differences within the medial prefrontal subsystem of the default network, with less temporal coupling of this network during AM retrieval in PTSD relative to controls. These findings suggest that the spatial and temporal characteristics of the default and control networks potentially differ in a PTSD group versus healthy controls and contribute to altered recall of personal memory.

Keywords PTSD · Episodic memory · Default network · Control network · Independent-component analysis · Anxiety · Functional connectivity · Hippocampus · Amygdala

Functional neuroimaging studies of posttraumatic stress disorder (PTSD) have observed consistent differences during emotional tasks in the recruitment of several brain regions, such as the medial prefrontal cortex (PFC), medial temporal lobe (MTL), and posterior midline regions (Etkin & Wager, 2007; Shin, Rauch, & Pitman, 2006), which overlap with the regions typically recruited during autobiographical memory (AM) retrieval (Cabeza & St. Jacques, 2007). Furthermore, PTSD studies have also shown that the functional connectivity between these regions is altered (e.g., Bluhm et al., 2009; Lanius et al., 2010; St. Jacques, Botzung, Miles, & Rubin, 2011), involving increases and/or decreases between these regions, depending on the nature of the task. Overlap among the functional correlates of AM retrieval and PTSD is consistent with behavioral studies that have reported increased reliving and emotional intensity in PTSD during retrieval of personal AMs that are not trauma-related (Rubin, Boals, & Berntsen, 2008; Rubin, Dennis, & Beckham, 2011). Thus, it is critical to consider the neural mechanisms underlying AM retrieval, which include a wide variety of personal memories in addition to memory for the trauma more specifically. Moreover, avoiding strong emotional and relived memories is a key symptom of PTSD (American Psychiatric Association, 2000). Whether such changes in neural activity and functional connectivity relate to potential differences in the contributions of large-scale neural networks supporting cognition in PTSD is largely unknown.

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Several neural networks have been identified in the brain during passive rest states (e.g., Damoiseaux et al., 2006), and some of these networks are also engaged during memory encoding of naturalistic events (e.g., Botzung, LaBar, Kragel, Miles, & Rubin, 2010) and AM retrieval (St. Jacques, Kragel, & Rubin, 2011). One of the most studied networks is the default network (Gusnard & Raichle, 2001; Raichle et al., 2001; for a review, see Buckner, Andrews-Hanna, & Schacter, 2008), a pattern of coherent brain activity first identified during passive rest and shown to be affected in PTSD (Bluhm et al., 2009; Lanius et al., 2010). Andrews-Hanna, Reidler, Sepulcre, Poulin, and Buckner (2010) recently showed that the default network comprises a medial PFC subsystem associated with self-relevant and affective processes, and an MTL subsystem linked to memory-based scene construction. Thus, it is not too surprising that the default network overlaps with and is actively recruited during AM retrieval (Spreng & Grady, 2010; St. Jacques et al. 2011c), in which self-referential and mnemonic processes are essential components. The default network is not, however, the only neural network that contributes to AM retrieval. For example, we (St. Jacques et al. 2011c) found that AM retrieval in healthy young adults is supported by frontoparietal and cinguloopercular networks, in addition to the medial PFC and MTL subsystems of the default network. The frontoparietal and cinguooperculum networks are associated with controlled processes (Dosenbach et al., 2007; Seeley et al., 2007), such as flexible and goal-directed cognition, and they couple with the default network to support AM functions (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010; St. Jacques et al. 2011c). Furthermore, many of the neural regions that show structural and functional changes in PTSD overlap with these control networks (Etkin & Wager, 2007; Shin et al., 2006).

In the present functional MRI (fMRI) study, we report a reanalysis of a previous study that employed a univariate approach (St. Jacques et al. 2011a) in order to examine the influence of PTSD on the engagement of neural networks during AM retrieval. The previous study employed a parametric modulation analysis technique to examine how neural activity sensitive to emotional intensity ratings differed during memory construction and elaboration in PTSD versus controls. In the present study, we used the multivariate technique of independent-component analysis (ICA; Calhoun, Adali, Pearlson, & Pekar, 2001b) to specify the temporal and spatial properties of the large-scale networks contributing to AM retrieval in PTSD versus healthy controls, collapsed across memories of different emotional qualities. Such analyses begin by assembling large-scale networks of voxels that show synchronized activity, rather than the more common univariate analyses that involve first locating areas that differ in activity and then examining connectivity among those areas. While both methods can make valid claims about connectivity, multivariate techniques allow for simultaneous analysis of the multiple brain regions comprising a network, rather than focusing on single brain regions in isolation, and more closely resembles how the brain is thought to support cognition (Fuster, 2009; Rubin, 2006). Furthermore, univariate techniques typically rely on subtraction paradigms that emphasize differences from a control task, which may obscure networks that functionally contribute to a particular task (Nyberg & McIntosh, 2001). Importantly, previous functional neuroimaging studies have shown that multivariate approaches can reveal novel information concerning AM retrieval, when compared to more standard univariate analyses (Svoboda, McKinnon, & Levine, 2006). At a more basic statistical level, univariate analysis is based on the level of activity in individual voxels, whereas multivariate analysis is based on correlations in activity between voxels; there is no necessary statistical relationship between these two forms of analysis, and therefore between the conclusions that might be drawn from them. Thus, it will be critical to apply such multivariate techniques in order to fully understand the neural mechanisms supporting AM in PTSD. Given the overlap between the brain regions affected in PTSD and the default and control networks contributing to AM retrieval, we explored the hypothesis that PTSD would affect both the temporal and spatial extents of these networks.

Method

Participants

We recruited young adult participants from Duke University (range of 18–35 years of age), and all testing occurred at Duke University. A database of healthy young adults who had expressed interest in participating in fMRI research studies was used to recruit the participants in the control group. The inclusion criteria for the control group followed the procedures that we have routinely used in behavioral studies in the Durham Veterans Association Medical Center (VAMC), which do not include previous trauma. This allowed us to examine the effect of PTSD versus a control group that was a random sample rather than one that was resilient to PTSD. The participants in the PTSD group were recruited from advertisements seeking volunteers who had been exposed to a traumatic event and from a prescreen test administered during a large group screening. The Clinician Administered PTSD Scale (CAPs) was used to determine PTSD diagnostic status in this group (Blake et al., 1995; Weathers, Keane, & Davidson, 2001). All participants in the PTSD group met the DSM-IV-TR (American Psychiatric Association, 2000) criteria, as measured by highly trained, master's-level clinicians who were experienced in giving the

CAPS in a research setting at the Durham VAMC. Each group comprised 19 participants. All of the participants reported that they were not taking any medication known to affect cognitive function (e.g., antidepressants, benzodiazepines, or any other psychiatric medication). Thus, the participants in both groups were not taking psychotropic medications. The investigation was carried out in accordance with the latest version of the Declaration of Helsinki, and participants gave written informed consent for a protocol approved by the Duke University Institutional Review Board. Five controls and four participants in the PTSD group were excluded from the analyses because of technical issues (e.g., no key responses recorded) or problems with completing the task as instructed (e.g., falling asleep, not following instructions). Thus, the reported results are based on the data from 14 controls and 15 PTSD participants.

Demographic and psychometric data were obtained in a separate session within one week of the scanning session (see Table 1; as reported in St. Jacques et al. 2011a). As expected, the PTSD group had higher scores on the PTSD Check List (PCL; Weathers, Litz, Herman, Huska, & Keane, 1993) when compared to the control group. The most common categories of traumatic events that the participants mentioned in response to the PCL were the death, attempted or actual suicide, or severe illness of a friend or family member (PTSD = 3, controls = 4), interpersonal issues (PTSD = 1, controls = 5), problems in academic or work environment (PTSD = 1, controls = 3), assault or abuse (PTSD = 4, controls = 0), motor vehicle accident (PTSD = 2, controls = 1), other (PSTD = 1, controls = 1), and not enough information to classify (PTSD = 3, controls = 0). It is important to note that the PCL was not used for diagnostic purposes, but was included for comparison between the groups. The PTSD group also had higher scores on the Beck Depression Index (BDI-II; Beck, Steer, & Brown, 1996) when compared to controls. No group differences emerged (all *p*s > .05) in proportions of women (PTSD = 11, controls = 7), years of age, years of education, the full Weschler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999), verbal fluency (FAS), or categorical fluency (animal names and supermarket items).

Materials

The retrieval cues to elicit AMs consisted of 60 emotionally arousing words selected from the Affective Norms for English Words (ANEW) database (Bradley & Lang, 1999), which included 30 positive (valence = 7.93, *SD* = 0.45; arousal = 5.96, *SD* = 0.83) and 30 negative (valence = 2.17, *SD* = 0.52; arousal = 6.00, *SD* = 1.03) words that were equally arousing. Auditory cue words were created by recording the words in a female voice and were constrained to equal durations of 1 s.

Procedure

A generic-cue-word method (Rubin, Schrauf, & Greenberg, 2003), frequently used in functional neuroimaging studies in healthy participants (Cabeza & St. Jacques, 2007), was employed to elicit AMs during fMRI scanning. Because the focus here was to examine the neural mechanisms associated with observed changes in the voluntary recall of AM (Rubin, Berntsen, & Bohni, 2008, Rubin et al., 2008, 2011), rather than to specify differences between trauma- and non-trauma-related personal memories in PTSD, this method allowed us to query a wide variety of memories. The procedure was similar to that of Daselaar et al. (2008; see also Greenberg et al., 2005). During scanning, participants heard an auditory cue word and were asked to use it to

Table 1 Participant variables by groups

	M		*SD*		
	Controls	PTSD	Controls	PTSD	*t*(27)
Age (years)	24.43	22.21	3.73	4.23	1.47
Education (years)	16.50	14.70	2.28	2.56	1.95
PCL[†]	27.93	49.00	7.99	12.94	−5.19*
BDI	3.93	16.86	3.29	11.00	−4.22*
WASI–Full IQ	122.36	121.50	7.66	10.14	0.25
WASI–Verbal IQ	120.93	123.93	7.87	11.44	−0.81
WASI–Performance IQ	118.14	114.72	7.49	10.17	1.01
Verbal fluency	47.43	51.36	10.87	10.49	−0.97
Categorical fluency	23.57	27.50	6.69	6.00	−1.63

*$p < .001$

[†] $df = 26$

search for an AM. Participants were instructed to covertly recall a unique AM for each cue word with specific spatio-temporal coordinates. They indicated when a specific AM was found by making a response on the button-box, and then continued to elaborate on the retrieved event in as much detail as possible for the rest of the trial. Then, 30 s following the onset of the auditory cue, participants were given auditory instructions to rate the amounts of emotion (*negatively arousing* to *positively arousing*) and reliving (*low* to *high*) associated with the memory on an 8-point scale. Rating responses were self-paced (up to 6 s) and separated by at least 0.5 s, and the order was counterbalanced between participants. We included six functional runs, with ten memory cues in each run (five positive and five negative words), and an intertrial interval of at least 1.5 to 7.5 s. During the duration of the run, participants were instructed to keep their eyes closed, so that any potential effects of visual imagery were not confounded by external attention to the stimulus.

Postscanning, participants were asked to provide a short title for the memory that they had retrieved during scanning and then to answer additional questions on a subset of the AM questionnaire (e.g., Rubin et al., 2003). Participants were asked to *date* when the event had occurred (e.g., *last day* to *>10 years ago*); to indicate the amount of *vividness*, or how clearly the event was remembered; the *perspective*, or whether the memory was seen through their own eyes or through the eyes of an outside observer; the *significance* of the memory; and the *physiological* response during retrieval (e.g., heart pounding). Also, given that AM comprises different types of events (Brewer, 1986), we asked participants to indicate whether the type of memory retrieved was a unique event (referring to a particular time and place), a repeated event (memory for an event with multiple occurrences), an extended event (occurring longer than one day), or semantic information (longstanding facts about one's own life; Williams, 1995).

fMRI methods

Image acquisition

Scanning was conducted using a 4-T GE magnet. Auditory stimuli were presented using headphones, and behavioral responses were recorded using an eight-button fiber-optic response box (Resonance Technology, Northridge, CA). Head motion was minimized by using foam pads and a headband. Anatomical scanning started with a T1-weighted sagittal localizer series, and then 3-D fast, spoiled, gradient echo recalled (SPGR) structural images were acquired in the coronal plane (256^2 matrix, TR = 12.3 ms, TE = 5.4 ms, flip angle = 20º, FOV = 240, 68 slices, 1.9-mm slice thickness). Functional images were subsequently acquired using an interleaved inverse spiral sequence (64^2 image matrix, TR = 2,000 ms, TE = 6 ms, flip angle = 60º, FOV = 240, 34 slices, 3.8-mm slice thickness).

Image preprocessing

Image preprocessing and analyses were performed using statistical parametric mapping software in MATLAB (SPM5; Wellcome Department of Imaging Neuroscience). The functional images were corrected for slice acquisition order, realigned to correct for motion artifacts, and then spatially normalized to a standard stereotactic space, using the template implemented in SPM5. Subsequently, the functional images were spatially smoothed using an 8-mm full-width-at-half-maximum isotropic Gaussian kernel.

Independent-component analysis (ICA)

ICA was used to determine the spatially distinct networks contributing to AM retrieval (for conventional analysis using a general linear model, see St. Jacques et al. 2011a), as implemented using the Group ICA of fMRI Toolbox (GIFT; Calhoun, Adali, Pearlson, & Pekar, 2001a). This method involves performing ICA on functional data across every participant and then creating a series of spatial maps and associated time courses for the group. Back reconstruction is then used to create individual time courses and spatial maps from each participant's functional data. This process was performed separately for each group. Conducting separate ICAs on each group strikes a balance between having a common model and combining multiple single-participant ICAs. A similar approach has been used to characterize alterations in memory-related networks between healthy aging, mild cognitive impairment, and Alzheimer's disease (Celone et al., 2006). The number of components in each group was estimated to be 30 using the minimum-description-length criteria (Li, Adali, & Calhoun, 2007). The amplitudes of the individual time courses and spatial maps were calibrated for comparison across participants, by regressing the back-reconstructed time courses from voxels with maximal spatial weights for each component, and scaling to reflect percentage change from the mean signal, as implemented in GIFT.

Component identification

Components with time courses related to the experimental design were identified using multiple regression, conducted separately within each group. AM retrieval operations were modeled by convolving stimulus functions with the canonical hemodynamic response. This model, implemented in SPM5, had separate regressors for the cue, construction, response, elaboration, and rating aspects of the task. The stimulus functions varied between regressors as either zero-duration Dirac delta functions (for cue, response, and

ratings) or as variable-duration boxcar functions (for construction and elaboration) that depended on the time of the motor response. The primary goal of the present study was to examine differences in the components associated with construction and elaboration phases of AM retrieval in healthy controls, as compared to those with PTSD. We conducted a regression analysis, using the temporal sorting tool in GIFT, to determine the β weights associating the components with construction and elaboration phases separately. One-sample t tests on these β weights showed four components that were significantly related ($p < .001$) to the construction and/or elaboration phases in healthy controls. As our goal was to examine alterations in the spatial and temporal characteristics of the networks supporting AM in PTSD, a spatial cross-correlation of component averages for each group was performed, yielding four components in the PTSD group that were highly similar (rs > .80) to those in the controls. No other components in the PTSD group were significantly related ($p < .001$) to the AM task. These four components were subsequently assessed in order to examine differences in the spatial and temporal characteristics between the PTSD and control groups.

Spatial comparison

To assess group differences in the spatial aspects of the components, the individual spatial maps were examined in a two-sample t test implemented in SPM5. To ensure that the comparisons of spatial maps reflected differences in network weighting, as opposed to differences in mean signal amplitude within a region (which would be better suited to univariate approaches), masks were separately created for each group and then combined using a conjunction approach. This procedure was done in three steps: First, a mask of all voxels that exceeded the mean activity were created for each participant; next, ICA was performed separately for each group, using the methods outlined above; and finally, conjunction of the two group-level masks was performed in order to reduce bias from differences in the initial masking procedure. Statistical comparisons of the spatial weights were controlled for multiple comparisons using a false-discovery-rate corrected p level of .05 (Genovese, Lazar, & Nichols, 2002) and >5 voxels. Given the a priori role of the amygdala in AM retrieval and our hypothesis regarding its differential recruitment in PTSD (Etkin & Wager, 2007; Shin et al., 2006), we conducted an additional region-of-interest (ROI) analysis on the results of the two-sample t test using the Talaraich Daemon Atlas (Lancaster, Summerlin, Rainey, Freitas, & Fox, 1997; Lancaster et al., 2000) implemented with the PickAtlas software (Maldjian, Laurienti, Kraft, & Burdette, 2003). The multiple-comparison correction was relaxed for the amygdala ROI (uncorrected $p = .05$).

Temporal comparison

To assess group differences in the temporal aspects of the components, we examined the relationship between the independent components and the temporally distinct phases of AM retrieval by conducting a series of Phase (construction, elaboration) × Group analyses of variance (ANOVAs) on the β weights from the ICA. Additionally, to further interrogate temporal differences, we examined the poststimulus time courses of the components, using a window of 30 s to encompass the construction and elaboration phases, by performing cue-locked event averaging, as implemented in GIFT. Separate temporal regressions conducting by means of a 2 × 2 ANOVA of valence (positive, negative) and phase (construction, elaboration) did not reveal an effect of valence within either group; thus, the results are presented across both positive and negative trials.

Network–PCL correlation

We conducted a correlation analysis in order to examine the relationship between network activity and individual differences in PTSD symptomatology. For each network, we computed neural activity on the basis of the area under the curve of the poststimulus time courses, and then examined the correlation with PCL scores while controlling for group.

Network–behavior regression

In order to examine the relationship between network activity and autobiographical characteristics as they potentially varied across the groups, we conducted multiple-regression analyses. For each network, we computed neural activity on the basis of the area under the curve of the poststimulus time courses and regressed this against group, emotional intensity, memory perspective, and the two-way interactions. We chose to focus on the contributions of emotional intensity and memory perspective because these variables differ in PTSD (e.g., Rubin et al. 2008b). Reliving was not included in the multiple-regression analyses due to issues of multicollinearity with emotional intensity. We note that substituting intensity with an interaction term with reliving produced nearly identical results, but for simplicity the reported results are shown for intensity only.

Results

Behavioral results

Participants were able to recall an event matching the cue on more than 97 % of the trials. The PTSD group ($M = .11$, $SD = .11$) recalled a greater proportion of memories associated with the stressful event identified in the PCL than

did the control group (M = .04, SD = .03), $t(25) = -2.35$, $p < .05$.[1] We found no group differences (all ps < .05) in reaction times to retrieving an AM (PTSD = 6.53 s, SD = 1.83; controls = 6.51 s, SD = 2.16), in the online ratings of reliving (PTSD = 5.35, SD = 0.68; controls = 5.03, SD = 1.06), or in emotional intensity (PTSD = 2.54, SD = 0.10; controls = 2.50, SD = 0.08). Postscan ratings of vividness (PTSD = 4.68, SD = 0.71; controls = 4.67, SD = 0.78), significance (PTSD = 3.40, SD = 0.53; controls = 3.00, SD = 0.81), and physiological response (PTSD = 2.61, SD = 0.78; controls = 2.30, SD = 0.98) also did not differ between groups. Furthermore, the date and type (i.e., memory specificity) of the memory did not differ between the groups (for full report of the behavioral results, see St. Jacques et al. 2011a). However, as expected (Rubin et al. 2008a), the perspectives from which the memories were retrieved differed between the two groups. As compared to the control group (own eyes = 5.75, SD = 0.84; observer = 2.39, SD = 0.92), memories retrieved by the PTSD group (own eyes = 4.86, SD = 1.22; observer = 3.23, SD = 1.18) were recalled less from the perspective of the participant's own eyes, $t(27) = 2.29$, $p < .05$, and more from an observer's perspective, $t(27) = -2.13$, $p < .05$.

fMRI results

Independent-component analysis

ICA revealed four components that were related to the construction and elaboration of AMs in the control group (see also St. Jacques et al. 2011c). These components were labeled according to their anatomical locations, and included frontoparietal, cinguloopercular, medial prefrontal cortex, and medial temporal lobe networks (see Fig. 1a). The four networks correspond to large-scale neural networks previously observed using both ICA (e.g., Botzung et al. 2010a) and other task-related (e.g., St. Jacques, Conway, Lowder, & Cabeza, 2011) and resting-state (e.g., Andrews-Hanna et al., 2010; Dosenbach et al., 2007) functional connectivity analyses. Importantly, the spatial cross-correlation values for each of the individual components revealed a high degree of similarity with four components identified independently in the PTSD group (see Table 2). Thus, similar networks contributing to AM retrieval were recruited in both the control and PTSD groups.

Spatial comparisons

Although both groups recruited similar networks during AM retrieval, the comparison of the spatial weightings within each network revealed several group differences (see Table 3 and Fig. 2). First, within the frontoparietal network, the PTSD group showed decreased component weights in the precuneus relative to controls. Second, within the cinguloperculum network, the PTSD group had decreased spatial weightings in the dorsal anterior cingulate cortex (dACC) as compared to controls. Third, within the medial PFC network, the PTSD group showed decreased spatial weightings in posterior midline and superior temporal cortex relative to controls. Finally, the spatial comparison within the MTL network revealed differential spatial weightings in the right amygdala, parietal cortex, and occipital cortex: The PTSD group had increased spatial weighting in the amygdala, but decreased weightings in the retrosplenial cortex, posterior cingulate, and parieto-occipital cortex when compared to controls.

Temporal comparisons

Examining differences in task relatedness showed two networks that had main effects of phase, one with a main effect of group, and no interactions (see Fig. 1b). The frontoparietal network showed a main effect of phase, $F(1, 28) = 5.55$, $p < .05$, indicating that activity in this component was associated more with construction than with elaboration. Similarly, the cinguloopercular network showed a main effect of phase, $F(1, 28) = 3.68$, $p < .05$, indicating that this component also contributed during construction but not elaboration. We found no main effects or interactions in the MTL network, indicating that activity within this network was equally associated with construction and elaboration phases in both groups. Finally, in the medial PFC network, no main effect of phase or interaction emerged, indicating that activity here was equally associated with construction and elaboration phases across the groups. However, a main effect of group was apparent, $F(1, 28) = 12.58$, $p < .001$, which showed that the medial PFC network was less associated with AM retrieval in the PTSD group than in controls. Cue-locked component time courses averaged across the participants in each group are shown in Fig. 1c.

Network–PCL correlation

Correlation analyses did not reveal any significant relationships between PCL scores and network activity after controlling for group (all ps > .05). These results suggest that individual differences in PTSD symptomatology were not related to network activity.

Network–behavior regression

Multiple-regression analyses revealed a significant relationship between the characteristics of autobiographical experience and neural activity in two of the networks. Within the

[1] Data were missing from two participants in the PTSD group due to experimenter error. Thus, the reported results for this analysis are based on 13 participants in the PTSD group and 14 participants in the controls.

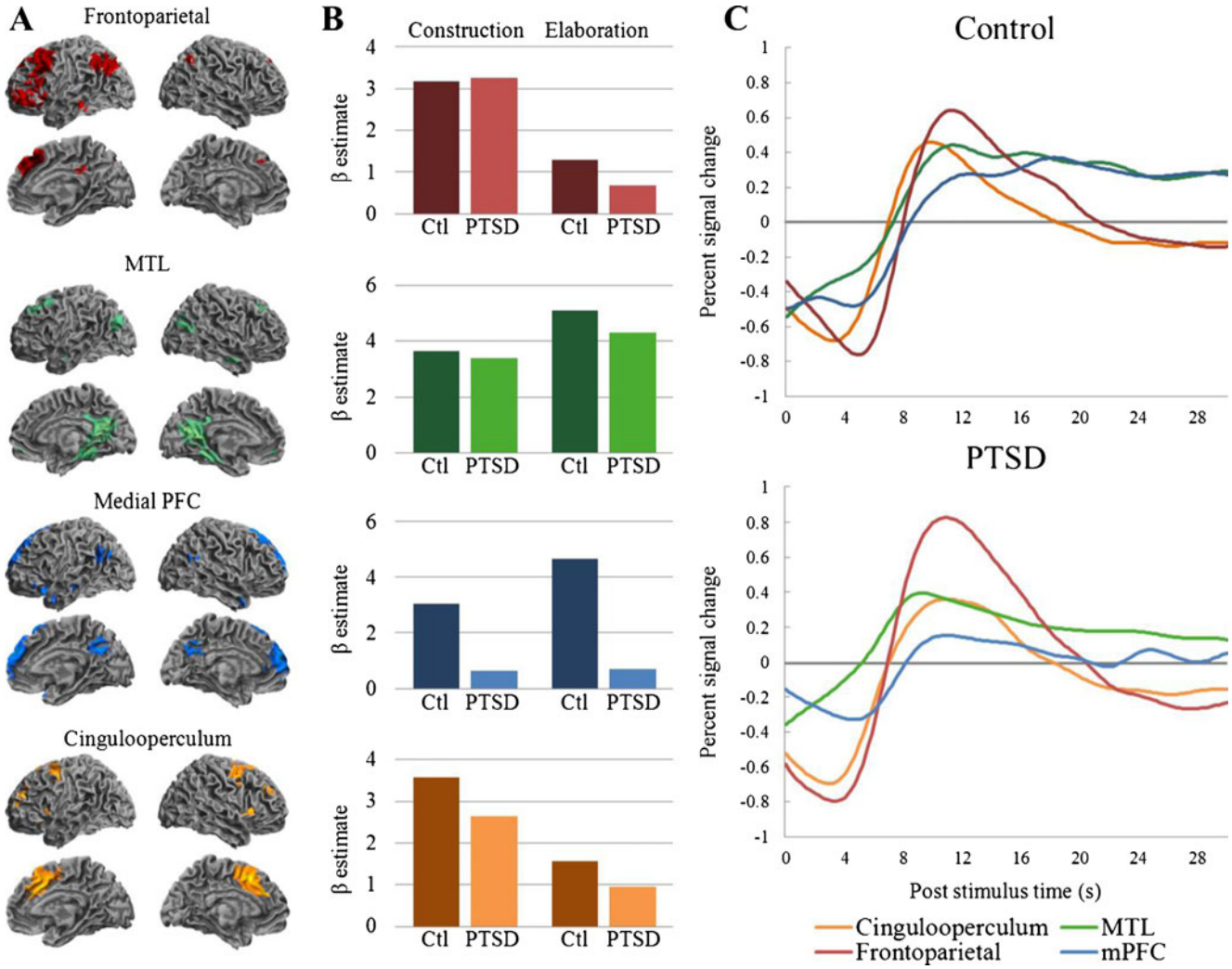

Fig. 1 Temporal comparison of networks and tasks in the PTSD and control groups. **a** Spatial distributions of the four components. The depicted activations reflect conjunctions of network patterns of activation in each group at $p < .05$, corrected for multiple comparisons. **b** Task-relatedness of component activity to the construction and elaboration task phases. The vertical axis depicts z scores of β weights indicating similarity between the component time courses and modeled activity for each phase. ANOVAs on the β weights revealed a main effect of phase in the cinguloopercular and frontoparietal components, as well as a main effect of group in the medial prefrontal cortex (PFC) component. **c** Cue-locked component time courses, averaged across the participants in each group, in units of percent signal. MTL, medial temporal lobe; Ctl, control group; PTSD, posttraumatic stress disorder group; mPFC, medial prefrontal cortex

frontoparietal network, the multiple R for regression was statistically significant, $F(5, 23) = 3.65$, $p < .05$, R^2 adjusted = .32. We found a significant Group × Emotional Intensity interaction, $\beta = -59.15$, $t(23) = -3.06$, $p < .01$, that

Table 2 Independent-component analysis

Network	r	Control		PTSD	
		Construction	Elaboration	Construction	Elaboration
Cinguloopercular	.83	5.03**	2.06	3.42*	1.45
MTL	.82	5.19***	9.53***	4.69**	6.88***
Medial PFC	.80	4.08*	7.95***	0.33	1.22
Frontoparietal	.84	4.27**	1.77	4.45**	0.32

r spatial correlation of components between groups

In the table, t values are reported. *$p < .01$, **$p < .001$, ***$p < .0001$

Table 3 Spatial comparison of networks

Region	BA	MNI Coordinates			Voxels	*z* Value	% Signal Change	
		x	*y*	*z*			Control	PTSD
Medical PFC Network								
PTSD < Controls								
Posterior midline	7/31	0	−68	38	89	5.01	2.20	0.22
Superior temporal cortex	22/21	60	−49	8	18	4.93	0.72	−0.17
PTSD > Controls								
No significant differences								
MTL Network								
PTSD < Controls								
Restrosplenial cortex	29/30	4	−45	0	22	5.09	1.34	−0.15
Parieto-occipital cortex	31/18	23	−64	19	37	4.94	1.26	0.20
	31/18	−23	−68	19	14	4.06	0.84	0.20
Posterior cingulate	31	−8	−68	19	6	3.86	2.52	1.16
PTSD > Controls								
Amygdala*	–	30	−4	−19	9	2.64	−0.17	0.12
Frontoparietal Network								
PTSD < Controls								
Precuneus	7	−15	−79	46	6	4.45	−0.05	0.69
PTSD > Controls								
No significant differences								
Cinguloopercular Network								
PTSD < Controls								
Dorsal ACC	32	4	38	23	11	5.34	0.24	1.34
PTSD > Control								
No significant differences								

BA Brodmann's area; *MNI* Montreal Neurological Institute; *PTSD* posttraumatic stress disorder; *PFC* prefrontal cortex; *MTL* medical temporal lobe; *ACC* anterior cingulate cortex. * Region-of-interest analysis

was reflected by a significant effect of emotional intensity in the control group, $\beta = 47.27$, $t(23) = 3.18$, $p < .005$, but not in the PTSD group, $\beta = -11.88$, $t(23) = 1.55$, $p = .35$. Thus, within the control group, increases in emotional intensity predicted neural activity in the frontoparietal network, but a similar relationship between emotional intensity and frontoparietal network activity was not found in the PTSD group. The Perspective × Group interaction and the main effects of group and perspective were not significant predictors of neural activity within the frontoparietal network (all *p*s > .05).

Within the MTL network, the multiple *R* for regression was also statistically significant, $F(5, 23) = 4.36$, $p < .01$, R^2 adjusted = .38. We found that memory perspective predicted neural activity equally across both groups, $\beta = 13.98$, $t(23) = 2.52$, $p < .05$, which indicated that memories retrieved from a first-person versus a third-person perspective recruited greater network activity in the MTL network. Group also predicted neural activity in the MTL network, $\beta = -14.83$, $t(23) = -2.07$, $p = .05$, with less neural recruitment of the MTL network in the PTSD versus the control group. Emotional intensity and the Emotional Intensity × Group interactions were not significant. No significant relationships emerged between AM characteristics and the remaining networks. However, within the medial PFC network, the multiple *R* for regression was statistically significant, $F(5, 23) = 5.26$, $p < .005$, R^2 adjusted = .43. This was reflected by a significant main effect of group, $\beta = -42.36$, $t(23) = -3.87$, $p < .001$, indicating that network activity in the medial PFC was reduced in the PTSD group when compared to controls.

Discussion

In the present study, we examined the large-scale neural networks contributing to AM retrieval in PTSD and controls. The data revealed that the PTSD group recruited similar neural networks during the recall of personal memories, including default-network subsystems (medial PFC

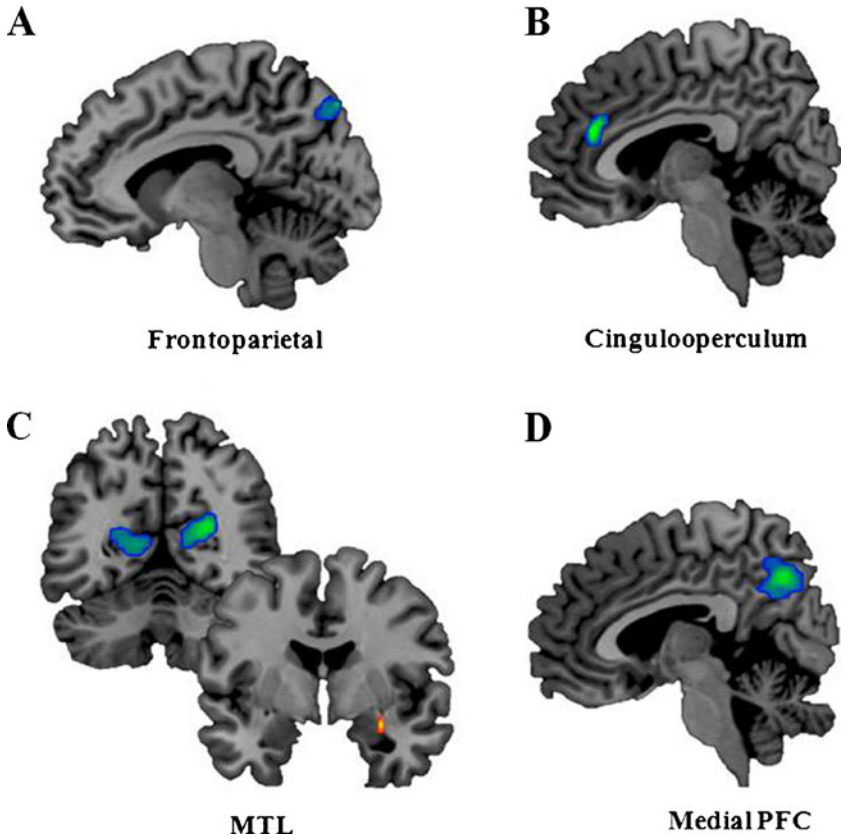

Fig. 2 Differences in spatial weightings of the networks between PTSD and control groups. The statistical maps are thresholded at $p < .05$, corrected for multiple comparisons. Multiple-comparison correction was relaxed for the amygdala. **a** In the frontoparietal network, decreased spatial weighting was evident in the precuneus for PTSD versus controls. **b** In the cinguloopercular network, we found decreased spatial weighting in the anterior cingulate in PTSD versus controls. **c** In the medial temporal lobe (MTL) network, as compared to controls, the PTSD group had decreased spatial weighting in bilateral parieto-occipital lobes, and increased spatial weighting in the right amygdala. **d** In the medial prefrontal cortex (PFC) network, decreased spatial weighting emerged in the posterior cingulate in PTSD as compared to controls

and MTL networks) and control networks (frontoparietal and cinguooperculum networks). Despite general similarities in network identification, however, differences emerged in the spatial and temporal characteristics of these networks in PTSD. First, we found spatial differences in the contributions of anterior and posterior midline across the networks, and of the amygdala in particular, for the MTL network. Second, temporal differences were apparent in the relationship between the medial PFC network and AM retrieval in PTSD relative to controls. We discuss each of these findings below.

Spatial comparison of networks

Although the networks identified in the PTSD group were largely similar to those identified in the control group, important group differences were present in the spatial characteristics of these networks. Within the MTL network, we found a greater contribution of the amygdala in the PTSD than in the control group. Previous functional neuroimaging studies of PTSD using univariate analysis have revealed hyperactivity in the amygdala and changes in amygdala–medial-PFC coupling (for a review, see Shin et al., 2006). For example, in a univariate analysis on these same participants, we (St. Jacques et al. 2011a) observed greater right amygdala recruitment during the construction of negatively intense AMs. Furthermore, greater functional coupling was observed between the amygdala and ventral medial PFC in emotionally intense negative AMs in PTSD versus controls. Here, we showed that the increased coupling with the amygdala in PTSD extends more widely across the entire MTL network and that greater coactivation with the amygdala in PTSD than in controls is also evident across a wide variety of AMs (see also Gilboa et al., 2004). Despite the amygdalar differences, emotional intensity did not differ between the groups, as was expected (e.g., Rubin et al. 2008b).

Although emotion is often considered an important component of AM, the amygdala is not frequently recruited during retrieval of autobiographical experiences (Svoboda et al., 2006). Indeed, in the present study, despite using

emotional word cues to elicit AMs, the amygdala did not contribute to the MTL network in healthy controls. One reason may be that the amygdala is selectively recruited only for particular phases of memory retrieval, and only for particularly strong emotional memories (Botzung, Rubin, Miles, Cabeza, & LaBar, 2010; Daselaar et al., 2008; Holland & Kensinger, 2013). For example, Daselaar et al. found that amygdala activity was modulated by the emotional intensity of AM retrieval during construction, but not during elaboration. This may be because, in healthy individuals, emotional responses that occur early during the course of AM retrieval are down-regulated or inhibited in order to access specific memory details during elaboration (Conway & Pleydell-Pearce, 2000; Philippot, Baeyens, Douilliez, & Francart, 2004). Thus, lack of amygdalar recruitment within the MTL network in healthy controls relative to PTSD may reflect differences in the ability to regulate emotional responses during the time course of AM retrieval.

Spatial comparisons within the MTL network also revealed less contribution from several posterior midline regions, including the retrosplenial cortex and parieto-occipital cortex, in the PTSD group. These regions contribute to visual details that enable the construction of a coherent scene (Hassabis & Maguire, 2007). In our previous study (St. Jacques et al. 2011a), we observed reduced neural recruitment of the occipital cortex in PTSD versus controls when retrieving emotionally intense AMs, and less involvement of the retrosplenial cortex in PTSD specifically during memory elaboration (but greater involvement in PTSD during construction). In the present study, we showed that retrieval of a wide variety of AMs—not necessarily emotionally intense memories—decreases coactivation of the retrosplenial cortex and parieto-occipital brain regions within the MTL network in PTSD. In sum, engagement of the MTL network in PTSD involves greater amygdala involvement coupled with decreased visual cortex involvement, suggesting that the emotional and visual processes contributing to memory retrieval are altered.

In both the MTL and medial PFC subsystems of the default network, we found reduced contributions of the posterior cingulate in PTSD when compared with controls. The posterior cingulate cortex is an important convergence zone allowing for interaction and integration among the medial PFC and MTL subsystems (Buckner et al., 2008; see also St. Jacques et al. 2011c). Several lines of evidence have suggested that the posterior cingulate is a pivotal node within the default network. For example, as compared to other regions within the default network, the posterior cingulate is the only region that directly interacts with all other nodes in the network (Fransson & Marrelec, 2008), it shows the highest metabolic activity (Gusnard & Raichle, 2001), and it is one of the first regions to be affected by disease (Minoshima et al., 1997). Perhaps because of its centrality, the posterior cingulate cortex is one of the most common seeds chosen in resting-state functional connectivity analyses. Previous PTSD studies showed reduced resting-state functional connectivity between the posterior cingulate and several regions of the default network, and that such changes were related to symptom severity (Bluhm et al., 2009; Lanius et al., 2010). The present results add to this literature by showing that PTSD-related alterations in posterior cingulate reflect the involvement of both subsystems of the default network and its active engagement during an AM retrieval task. The reduced involvement of the posterior cingulate in the default network recruited by the PTSD group may have contributed to differences in the function of this network during AM retrieval, perhaps by altering its interactions with other networks.

Interestingly, spatial comparisons among the networks also revealed differences within the control networks contributing to AM retrieval in PTSD. Within the frontoparietal network, there was a decreased contribution of the precuneus, whereas the cinguloopercular network showed decreased involvement of the anterior cingulate cortex. Functional changes in the recruitment of the posterior cingulate and precuneus were not evident in the previous, univariate analysis, suggesting that the multivariate approach can provide additional evidence regarding functional regions contributing to PTSD. Group differences in the spatial characteristics of neural networks may influence their temporal engagement during AM retrieval. We turn next to discussion of the temporal comparison of the networks.

Temporal comparison of networks

The temporal comparisons of network contributions to phases of AM retrieval were very similar across the groups, except for the medial PFC network. As in our previous analysis in healthy participants (St. Jacques et al. 2011c), the frontoparietal and cinguloopercular networks also contributed to greater extents to memory construction than to elaboration among the PTSD group. The frontoparietal and cinguloopercular networks support the adaptive deployment of controlled processes and the maintenance of goals (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Dosenbach et al., 2007; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008), both of which may be particularly important during the cue specification and memory search and construction components of the initial phase of AM retrieval. We also found that the MTL network was equivalently recruited in both groups across both construction and elaboration. Thus, it appears that PTSD does not generally affect the engagement either of controlled networks during construction or of the MTL network supporting mnemonic processes across the construction and elaboration of AM.

However, temporal engagement of regions within these networks, such as the amygdala and retrosplenial cortex, may be differentially associated with the construction versus the elaboration of AMs on a trial-by-trial basis, according to the emotional response associated with memory retrieval (St. Jacques et al. 2011a).

Group differences were only observed when considering the contribution of the medial PFC network to AM retrieval. We found that the PTSD group showed less engagement of the medial PFC network across both the construction and elaboration phases of AM retrieval. The medial PFC network supports self-referential and affective processes (Andrews-Hanna et al., 2010; St. Jacques et al. 2011b) that are closely linked to memory for autobiographical experiences (e.g., Brewer, 1986; Cabeza et al., 2004; Conway, 2005; Muscatell, Addis, & Kensinger, 2010). In healthy controls, the medial PFC network drives neural activations during AM retrieval (St. Jacques et al. 2011c), a finding consistent with the importance of the self in AM construction (Conway & Pleydell-Pearce, 2000).

It is important to point out that the lack of task-related correspondence with the medial PFC network does not necessarily suggest that the PTSD group did not activate this network during AM retrieval; rather, it reflects a failure to activate this network more than during the implicit baseline, the fixation period between trials. One potential explanation could be that the PTSD group activates the medial PFC network during fixation intervals due to continued self-reflection and affective processes related to previously retrieved memories. However, prior research examining resting-state functional connectivity has suggested that the integrity of the default network, encompassing the medial PFC subnetwork, is impaired in patients with PTSD (Bluhm et al., 2009). Further research will be needed to determine the exact nature of this failure of the PTSD group to activate the medial PFC network during functional tasks, such as AM retrieval, and its relationship to similar impairments in large-scale networks observed during rest.

Network–behavior regression

Individual differences in the characteristics of AM retrieval were found to predict recruitment of the MTL and frontoparietal networks. First, we found that memory perspective was associated with increased engagement of the MTL network, such that participants who experienced memory retrieval from the perspective of their own eyes recruited this network more. The associations between perspective and MTL network recruitment were similar across both groups and potentially reflect the involvement of this network in scene construction, because memories that are viewed from one's own perspective are more vivid and detailed (Rice & Rubin, 2009). Second, we found that the emotional intensity of memory was associated with increased engagement of the frontoparietal network in controls but not in PTSD. Emotion tends to be experienced earlier during AM retrieval (Daselaar et al., 2008), perhaps serving as a warning signal that triggers deployment of control processes that regulate affective responses in order to allow for detailed memory retrieval. Given the role of the frontoparietal network in adaptive control processes during memory construction, one interpretation of this finding is that PTSD participants do not modulate recruitment of top-down control processes on the basis of the emotional intensity experienced during memory retrieval. Thus, despite the lack of overall group differences during AM retrieval, emotional intensity may differentially contribute to engagement of the frontoparietal network in PTSD versus control participants.

Limitations

It is important to note that one potential limitation of the present study is that an additional trauma-exposed, non-PTSD group was not included. This may be particularly relevant for interpreting the group differences observed in the MTL network, because previous evidence has suggested that preexisting structural abnormalities in the hippocampus may predict vulnerability to PTSD following trauma exposure (Gilbertson et al., 2002) and that functional activity in the hippocampus predicts recovery from PTSD (Dickie, Brunet, Akerib, & Armony, 2011). An additional limitation is that the small sample size precluded the possibility of examining interactions with other factors that could have contributed to these findings, such as sex, and may have reduced the power for observing network correlations with individual differences in PTSD symptomatology. Future studies should include an additional control non-PTSD group that was trauma-exposed, as well as increasing the sample size of all groups, in order to address these issues.

Conclusions

In the present study, we found differences in both the spatial extent and task-related activation of the neural networks contributing to AM retrieval in PTSD. In particular, during AM retrieval, participants with PTSD activated the same four networks as did controls, including two that together comprise the default network; however, theoretically relevant differences emerged in the extents and task-related timings of these networks. First, we found spatial differences in the contributions of anterior and posterior midline across the networks, and of the amygdala in particular, for the MTL subsystem of the default network. Second, temporal differences were evident in the medial prefrontal subsystem of the default network, with less temporal

coupling between this network and AM retrieval in PTSD than in controls. These findings contribute to our understanding of the neural mechanisms supporting AM retrieval and of their relationship to PTSD by revealing functional differences in the spatial and temporal properties of the multiple neural networks that underlie AM.

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