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Different activation patterns for working memory load and visual attention load

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Abstract

Attention is a basic component of cognition, and is modulated by cognitive load. We aimed to map the common network that supports attentional load across different tasks using functional magnetic resonance imaging (fMRI). Twenty-two healthy volunteers performed two sets of tasks with graded levels of cognitive load: verbal working memory (WM) and visual attention (VA) tasks. For both tasks, increased cognitive load (WM-load and VA-load) activated a common network comprising parietal and occipital cortices, thalamus, and the cerebellum, indicating that these brain regions are involved in higher level of attention. The fMRI signals in the prefrontal cortices increased with WM-load but not with VA-load, suggesting that executive function is involved for the more demanding WM tasks but not for the more difficult VA tasks. Conversely, VA tasks activated more strongly an occipito-parietal network comprising the postcentral (PostCG) and the superior occipital (SOG) gyri, suggesting complex visual processing in this network.

Keywords

fMRI; memory; attention; brain activation

Introduction

Functional (Kanwisher and Wojciulik, 2000) and neuropsychological (Driver and Mattingley, 1998) studies support the concept that a wide variety of attention-demanding tasks may share a distributed frontoparietal network of brain areas. Studies on working (WM), episodic, and semantic memory that used positron emission tomography (PET) (Nyberg et al., 2003), and functional magnetic resonance imaging (fMRI) (Braver et al., 2001, Cabeza et al., 2002, Ranganath et al., 2003) in the same individuals found common activation patterns; specifically, some prefrontal regions are engaged during a range of memory tasks. fMRI studies of episodic retrieval (ER) and visual attention (VA) in the same set of subjects (Cabeza et al., 2003, Cabeza et al., 2004) also found a common fronto-parietal-cingulate-thalamic network for ER and VA, suggesting that the involvement of these regions during ER reflects general attentional processes.

Meta-analyses of WM and spatial attention (SA) data from the neuroimaging literature were used in the past to determine the similarities in activation patterns across these tasks (Smith

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and Jonides, 1997, Cabeza and Nyberg, 2000). However, comparisons between the different studies often have limitations, including nonequivalent baseline contrasts, intersubject variability in behavioral performance and blood oxygenation-level-dependent (BOLD) signal detection, and hardware and software-specific differences in signal acquisition and processing across research centers.

Only one prior study evaluated both verbal WM and SA tasks in the same set of subjects using fMRI (LaBar et al., 1999), and found common activations in a distributed network comprising frontal, temporal, and parietal cortices, the thalamus, and the cerebellum. Since the SA task had little WM requirement, and the WM task had no SA requirement, the overlapping activation patterns in those regions suggest a common dynamic shifting of attentional resources during the two tasks.

Recently, we used a set of verbal WM (*n*-back) tasks (Speck et al., 2000, Tomasi et al., 2005) and VA tasks that require the tracking of several (*n*) moving objects in a display (Jovicich et al., 2001, Tomasi et al., 2004) to evaluate the effect of the human immunodeficiency virus on brain activation (Chang et al., 2001, Ernst et al., 2002, Ernst et al., 2003, Chang et al., 2004, Tomasi et al., 2006). The tasks have graded levels of task difficulty to study the effect of cognitive load (Braver et al., 1997), and have minimal overlap of cognitive features. The VA paradigm requires covert attentional pursuit of *n* moving visual targets and does not have WM-load requirements. Conversely, the WM paradigm requires holding in memory the *n* most recently presented letters, but does not have VA-load requirements. Despite these differences, the tasks activate a common network that includes prefrontal, parietal, and occipital cortices, the basal ganglia, and the cerebellum. Since the networks involved in attention and working memory have limited capacity, it is important to determine if and how shared or distinct brain regions are allocated to support increased task difficulty (load) in these two cognitive domains. This question, however, has not been addressed, probably because of the intrinsic low power of third-level statistical analyses.

Therefore, we combined and re-analyzed several existing WM- and VA-fMRI datasets in order to map the common network that support attentional load across different task on the same set of subjects. Assuming that the WM task involves “working memory” and “attention shifting” cognitive components, and that the VA task involves “visual indexing” and “attention shifting” cognitive components, our goal was to identify the neural substrates of the common “attentional shifting” component, and the differential “working memory” and “visual indexing” components.

Results

Performance and reaction times

The average values of task performance and reaction time (RT) during fMRI are presented in Fig 1 for WM and VA tasks. The subjects were able to perform both tasks with high performance accuracy (>89%). For both tasks, increased cognitive load (WM: from 0-back to 2-back; VA: from 2-balls to 4-balls) reduced performance accuracy (p -value < 0.0001), but no difference was observed between the tasks (WM vs. VA). Reduced performance accuracy with increased cognitive load supports the increased difficulty of the tasks (Culham et al., 2001). Higher cognitive load increased RTs for WM tasks (p < 0.0001), but not for VA tasks; RTs were longer for VA than for WM.

WM- and VA-networks

WM tasks activated a network (Table 1; Fig 2 “WM”, red) that includes the prefrontal (PFC) cortex [inferior (IFG47; BA: 47), medial (medFG8), and middle (MFG9) frontal gyri], inferior (IPL40) and superior (SPL7) parietal lobes, IOG19, and FusG19, thalamus and cerebellum

[declive, uvula, and vermis], in agreement with our prior observations (Chang et al., 2001, Tomasi et al., 2005). VA tasks activated a network (Table 1; Fig 2 “VA”, red) that includes the same brain regions and additionally the MFG6, PostCG7, and SOG19, also in agreement with our previous studies (Jovicich et al., 2001, Chang et al., 2004, Tomasi et al., 2004). Figure 2 “Tracking” shows the differential activation patterns WM > VA and VA > WM. Brain activation was larger for VA compared to WM in the right SOG, and bilaterally in the MFG6, IPL, SPL, and the PostCG. However, brain activation for WM tasks was not larger than those for VA in any of the brain regions.

WM- and VA-load

Larger WM-load increased brain activation in left IFG, IPL, and IOG, and bilaterally in the medFG, MFG9, SPL, and FusG and the cerebellum (Fig 2 “WM”, green). VA-load effects were observed in the left SPL, thalamus, and IOG, and bilaterally in the FusG, IPL, SOG, IOG, and the cerebellum (Fig 2 “VA”, green). Common load effects were found in the FusG, SPL, IOG, IPL and the cerebellum (Table 1; Fig 2 “Common attention”, conjunctive analysis of WM-load and VA-load). The load-effect of VA was greater than that of WM in the right SOG and the left thalamus (Table 1; Fig 2 “Differential Load”, red). Conversely, the WM-load effect was larger in the left IPL and bilaterally in the MFG9 and medFG (Table 1; Fig 2 “Differential Load”, green).

ROI results

The ROI analyses of BOLD signals during WM and VA are summarized in Figure 3 and Table 2. Overall, the activated brain regions showed three relatively distinct response patterns: **(A)** For VA and WM tasks, increased cognitive load produced increased BOLD responses in the IPL, IOG, FusG, cerebellum, and thalamus ($p < 0.001$; Fig 3A). Mean BOLD signals in these regions did not differ between WM and VA tasks. Load-responses in the IPL and thalamus were highly correlated with load-responses in other regions during VA tasks, but poorly correlated during WM tasks (Table 2). **(B)** As shown in Fig 3B, increased task difficulty increased BOLD signals strongly in the IFG, MFG9, and medFG during WM tasks but weakly during VA ($p < 0.0001$; WM-load > VA-load, paired t -test). Load responses in the IPL and other regions in this sub network were highly correlated during WM tasks, but poorly correlated during VA tasks (Table 2). **(C)** Conversely, Fig 3c shows that BOLD responses in the PostCG and SOG were larger during VA ($p < 0.0005$) than during WM-tasks. fMRI signals in the SOG modulated with VA-load ($p = 0.02$) but not with WM-load. Load responses in the SOG and PostCG correlated better during VA tasks than during WM tasks. Load responses in this sub network were highly correlated with load responses in brain regions of the common attention network (FusG/IOG, IPL, and cerebellum) of BOLD responses

Discussion

This is the first within-subject comparison of load-dependent changes of brain activation during two different cognitive tasks. The main findings of the study are: a) increased cognitive-load (WM-load or VA-load) produced larger BOLD responses in a common network that includes the IPL, IOG/FusG, cerebellum, and thalamus, b) increased WM-load caused larger activation in a fronto-parietal network that includes the IFG, MFG9, medFG, and IPL; load effects in these regions were more pronounced for WM than for VA tasks, and c) only VA tasks activated the PostCG and produced significant load effects in the SOG.

Our finding of a common network for VA-load and WM-load, comprising the IPL, IOG/FusG, thalamus, and the cerebellum (see Figs 2a and 2b, and Table 1) is consistent with that observed in previous neuroimaging studies (Smith and Jonides, 1997, LaBar et al., 1999, Cabeza and Nyberg, 2000). Studies in rats (Burk and Mair, 2001, Chudasama and Muir, 2001, Newman and

Burk, 2005) and humans (Kinomura et al., 1996, Buchel et al., 1998, Guillery et al., 1998, Jovicich et al., 2001, Ackermann et al., 2004, Tomasi et al., 2004, Golla et al., 2005, Hazlett et al., 2005, Konarski et al., 2005, Machner et al., 2005, Richter et al., 2005, Ronning et al., 2005) carry out important attentional processing. This suggests that increased cognitive load involves increased attentional processing in these brain regions, regardless whether the task requires visuospatial attention or verbal WM skills. Our findings are generally similar and consistent with those reported by LaBar et al. (1999), but some differences are found, probably due to the differences between the tasks employed and the study design. First, the study by LeBar et al did not use tasks with increasing task difficulty (i.e. increasing cognitive loads). Second, this prior study compared the activation patterns between a similar WM task, but a different spatial attention task, as our current study. Third, we also found a significant overlap between brain regions activated during the WM and VA tasks, but the overlap between the networks associated with the increasing levels of difficulty (load effects) for WM and VA do not include prefrontal and temporal cortices. Thus, load manipulations in the present study, which specifically increased the attentional requirement, demonstrate that attention processing is localized more specifically in parietal and occipital cortices, thalamus and the cerebellum. Prior studies suggested that the thalamus and cerebellum might carry out important attentional processing, while parietal and occipital cortices may play a central role to process and store object information (Baddeley, 2003, Muller et al., 2003). Overall, the common activation patterns observed in this study may reflect shifting of attentional focus, irrespective of whether the shifts occur over space (VA) or time (WM), as suggested previously by LaBar et al (1999).

WM-load produced larger left-lateralized increases of brain activation than VA-load in the IPL, medFG, MFG9, and IFG (see Figs 2d, and Table 1). Association of the IPL activation with WM-load, but not VA-load, suggests a specific higher level of WM-function for the IPL; for instance as a phonological store function (Baddeley, 2003). Larger load-related responses in the IFG, medFG, MFG9&46 for WM compared to VA demonstrate greater involvement of the lateral prefrontal region in WM. This suggests that the IFG, medFG, and the MFG9&46 perform specific WM-processing in addition to general attentional processing, in agreement with previous studies (Manoach et al., 1997, Rypma and D'Esposito, 1999).

Findings of larger brain activation (BOLD signals) in the PostCG and SOG for VA tasks compared to WM tasks (Figs 2 "Tracking" and 3C; and Table 1) suggest specific VA processing in these brain areas. The object tracking methodology used in this work (Pylyshyn and Storm, 1988) is based on a pure attentional processing-technique called "visual indexing" (Sears and Pylyshyn, 2000). According to Pylyshyn (Pylyshyn, 1989) and Yantis (Yantis and Johnston, 1990), a small number of visual objects can be pre-attentively indexed or tagged and thereby accessed more rapidly by a subsequent attentional process. Bilateral load-dependent activation in the PostCG is frequently produced by motion tracking tasks (Culham et al., 1997, Culham et al., 1998, Culham et al., 2001, Jovicich et al., 2001, Chang et al., 2004); however, it is not observed in studies of sustained attention (Lawrence et al., 2003, Fassbender et al., 2004), selective attention (Le et al., 1998, de Fockert et al., 2001), visual search (Leonards et al., 2000), object recognition (Adler et al., 2001), attention to visual motion (Buchel et al., 1998), and orienting visual attention (Arrington et al., 2000).

Findings of strong cross-correlations of load-related BOLD responses in the IPL and thalamus and other brain regions during VA tasks suggests that the IPL and thalamus are the interconnection centers of the common attention network. Such connections are supported by studies in non-human primates showing that the thalamus (Middleton, 2000, Middleton and Strick, 2002) and the IPL (Clower et al., 2001) receive projections from many brain regions. Findings of higher cross-correlation of load-related BOLD responses during VA tasks than during WM tasks, between the IPL or thalamus and other brain regions, suggests greater

attention requirements for the VA tasks. Higher cross-correlations of load-related BOLD responses in the PFC and SPL for WM tasks than for VA tasks are in agreement with fMRI studies suggesting that the load-related connectivity between these regions may reflect greater demand for maintenance and executive processes during working memory processing (Honey et al., 2002).

In summary, we evaluated brain activation during WM and VA tasks with increasing levels of difficulty in the same set of subjects, using parametric fMRI methods at 4 Tesla. While the motion-tracking task had no WM requirement, and the WM task had no motion-tracking requirement, increased cognitive load (WM-load and VA-load) activated a large common network that includes the IPL, IOG/FusG, thalamus, and the cerebellum. This finding suggests that this network is even more specific for higher level attentional processing. Our study refines the findings from a previous fMRI study that evaluated the overlap in brain networks for WM and attention (LaBar et al., 1999). In addition, we observed that activation in a frontoparietal network comprising the IFG, medFG, MFG (BAs: 9) and the IPL was better associated with the WM-load than the VA-load, suggesting a greater involvement of the lateral prefrontal cortex during WM, especially in the IPL. Conversely, VA selectively activated an occipitoparietal network that includes the PostCG and the SOG, suggesting a specialized visual processing function in this network. These findings indicate that complex visual processing during visual attention might be carried out at an early stage of this network.

Methods

Subjects

Twenty-two healthy, non-smoking, right-handed volunteers (10 men and 12 women, age 30 ± 8 years, education: 16 ± 2 years) with normal vision participated in the study. Prior to the study, each subject signed a written informed consent, approved by our Institutional Review Board. Subjects were screened carefully with a detailed medical history, physical and neurological examination, blood and urine screening tests, to ensure they fulfilled all the study criteria. Inclusion criteria were: 1) age 18 years or older; 2) English as first language; 3) healthy and on no medications (except for vitamins); 4) ability to provide consent and willingness to participate in the study. Exclusion criteria were: 1) history of head injury with loss of consciousness > 30 minutes; 2) current or past drug abuse or dependence (including nicotine and alcohol) or positive urine toxicology (for cocaine, amphetamines, marijuana, benzodiazepines, and opiates); 3) any past or current medical or neuropsychiatric illnesses; 4) significant abnormalities on screening blood tests, including a complete blood count, a chemistry panel, thyroid function tests, a positive HIV test or hepatitis tests; 5) pregnancy (assessed by a urine test) or breast-feeding if female subjects; 6) any contraindications for MRI (e.g. metallic implants or claustrophobia).

Visual attention paradigm

Subjects performed a set of non-verbal visual attention tasks, which involved alternating blocks of mental tracking versus non-tracking of moving balls (Culham et al., 1998, Jovicich et al., 2001, Chang et al., 2004, Tomasi et al., 2004). The task blocks were composed of five “TRACK” and respond 12 seconds-long periods. During these periods, two, three, or four out of ten target balls were briefly highlighted, and then all balls started to move; the subjects' task was to fixate on the center cross and track the target balls as they moved randomly across the display (12° of the central visual field) for 10 seconds with instantaneous angular speed of 3° /second. The 10 balls moved in a simulated Brownian motion, and collided with, but did not penetrate, each other. At the end of “TRACK” periods, the balls stopped moving and a new set of balls was highlighted for 0.5 seconds; the subjects' task was to press a button if these balls were the same as the target set. This task has minimal spatial working memory component

because there is no delay between the last moving frame and the subsequent highlight. Button press events were used to record performance accuracy (the difference between right/hits and wrong/false alarm events) and reaction times (RT) during the fMRI tasks. After a 1 second delay (response window), the original target balls were then re-highlighted for 0.5 seconds to re-focus the subjects' attention on these balls. The control blocks were composed of five "DO NOT TRACK" periods. During these periods all 10 balls moved and stopped in the same manner as during "TRACK" periods; however, no balls were highlighted, and subjects were instructed not to track the balls, instead to view them passively; the use of this resting condition allowed us to control for the confounding effect of visual input activation.

Working memory paradigm

Three sequential letter tasks were used to evaluate working memory. Alphabetical letters (white) were flashed against a black background for 500 milliseconds, randomly at a rate of one per second. The subjects were instructed to press the button as fast as possible when they saw a letter (0-back task), when the current letter was the same as the one before (1-back task), or two before (2-back task). During each 30 seconds task period, five targets were presented at random time points. During the alternating resting period (30 seconds), nonsense characters were randomly flashed against the black background with the same size (9° of the central visual field), rate, color and luminance, and the subjects were instructed not to respond but to maintain fixation at the white center cross. By using this control condition, we minimize confounding activation in primary visual areas.

Subjects performed a brief training session (~10 minutes) of a shortened version of the tasks on a PC outside of the scanner to ensure that they understood and were able to perform the tasks adequately.

During fMRI, the stimuli were presented to the subjects on MRI-compatible LCD goggles connected to a personal computer. All response button events during stimulation were recorded to determine task performance and reaction times during fMRI. Task order was counterbalanced to minimize habituation effects. Half the studies started with WM tasks; the remaining studies started with VA tasks.

Data acquisition

Subjects underwent MRI in a 4 T whole-body Varian/Siemens MRI scanner, equipped with a self-shielded whole-body SONATA gradient set. The BOLD responses were measured as a function of time using a T2*-weighted single-shot gradient-echo EPI sequence covering the whole brain (TE/TR=25/3000 ms, 4 mm slice thickness, 1 mm gap, 48×64 matrix size, 4.1×3.1 mm in-plane resolution, time points: 84 for WM, and 124 for VA). Padding was used to minimize motion.

Data processing

The first four volumes of each time series were discarded to avoid non-equilibrium effects of the MR signal. The statistical parametric mapping package SPM2 (Wellcome Department of Cognitive Neurology, London UK) was used for subsequent analyses. The time series were realigned to the first volume to correct for head motion, which was limited to less than 1-mm translations and 1° -rotations for all 132 fMRI runs in the analysis. The realigned datasets were normalized to the Talairach frame using a voxel size of $3 \times 3 \times 3$ mm³, and smoothed using an 8-mm full-width-half-maximum Gaussian kernel. The general linear model (Friston et al., 1995) and a box-car design convolved with a canonical hemodynamic response function (HRF) were used to calculate the activation maps for each trial, using a fixed-effects model. The time series were band pass filtered with the HRF (as low pass filter) and a high-pass filter (cut-off frequencies: 1/126Hz for WM, and 1/256 Hz for VA).

Statistical analyses

A voxel-by-voxel repeated measures ANOVA was performed with six conditions (0-back, 1-back, 2-back, 2-balls, 3-balls, and 4-balls), using the mask of the combined network. The SPM statistical model “Full Monty” was used for this purpose. Activation maps for distinct and common neural networks were calculated using subtraction and conjunction contrasts. Clusters with at least 15 voxels (400 mm³) and $p < 0.05$ (corrected for multiple comparisons) were considered significant in group analyses (Friston et al., 1994), using a voxel-level threshold of $p = 0.05$ corrected by the family wise error (FWE). Masking and high statistical thresholds were used to control for potential power differences during estimation (fixed-effects) of BOLD responses between the tasks; the WM and VA tasks have different duration, and number of blocks, which could result in differential signal estimation errors across tasks.

Region-of-interest (ROI) analysis

To further validate the SPM results, functional ROIs with volume of 729 mm³ (cubic, 27 voxels) were defined at the cluster centers of brain activation (Table 1) to extract the average BOLD signal from these regions, using a customized program written in IDL (Research Systems, Boulder, CO). The position, shape, and size of the ROIs were invariant across subjects, tasks, and conditions. Additional cross-correlation analyses between load effects (differential BOLD responses; WM-load: “2-back” – “0-back”; VA-load: “4-balls” – “2-balls”) in the ROIs were performed across subjects to study potential interconnections in the networks. Statistical significance for ROI analyses was defined as $p = 0.05$ (uncorrected).

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Fig 1.
Performance accuracy and reaction times as a function of the cognitive load for visual attention and working memory tasks.

Fig 2.

The surface-rendered maps of brain activation showing areas that activated independently (red), and proportionally (green) to cognitive load, and regions activated by both tasks (yellow) (working memory “WM”, first column; visual attention “VA”, second column). Also shown are the common (third column) and differential (fourth column) load effects as well as the differential BOLD responses (“VA > WM”, fifth column). Sample size: Twenty-two healthy subjects; random-effects analyses. Color bars are the *T*-score windows. IFG: inferior frontal gyrus; MFG: middle frontal gyrus; medFG: medial frontal gyrus; FusG: fusiform gyrus; IPL: inferior parietal lobe; SPL: superior parietal lobe; PostCG: postcentral gyrus; SOG: superior occipital gyrus;

Fig 3.

average BOLD signals across subjects at specific ROIs for the visual attention (VA, dark-gray) and working memory (WM, light-gray) tasks in brain regions exhibiting (A) increased activation under increasing task difficulty for both tasks; (B) increased activation for the WM task only, and (C) activation for the VA task only. IFG: inferior frontal gyrus; MFG9: middle frontal gyrus BA 9; medFG: medial frontal gyrus; FusG: fusiform gyrus; IPL: inferior parietal lobe; SPL: superior parietal lobe; PostCG: postcentral gyrus; SOG: superior occipital gyrus; IOG: inferior occipital gyrus; Error bars represent standard errors.

Table 1

Location of major areas of brain activation in the Talairach frame of reference, and statistical significance of BOLD responses in these locations. Sample size: Twenty-two healthy subjects. Repeated measures ANOVA (random-effects) analyses; IFG: inferior frontal gyrus; MFG: middle frontal gyrus; medFG: medial frontal gyrus; FusG: fusiform gyrus; IPL: inferior parietal lobe; SPL: superior parietal lobe; PostCG: postcentral gyrus; SOG: superior occipital gyrus; IOG: inferior occipital gyrus; CER: cerebellum; BA: Brodmann area.

Brain Region	Side	x	y	z	VA	WM	T-scores VA Load	WM Load	VA>WM	VA-load > WM-load
IFG (BA47)	L	-36	15	-3	5.7*	8.0*	NS	3.9 [∇]	NS	NS
	R	27	18	0	6.1*	5.4*	NS	NS	NS	NS
MFG (BA6)	L	-24	6	60	8.8*	NS	NS	NS	5.3 [∇]	NS
	R	33	-12	57	4.0	NS	NS	NS	4.4*	NS
MFG (BA9)	L	-36	21	15	2.9*	7.7*	NS	5.9*	NS	NS
	R	39	15	18	7.9*	8.3*	NS	5.1*	NS	-4.8* -3.6 [∇]
medFG (BA8)	C	3	21	39	5.1*	7.0*	NS	3.9 [∇]	NS	-3.4 [∇]
FusG (BA19)	L	-39	-63	-6	8.7*	10.0*	4.9*	6.5*	NS	NS
	R	39	-66	-15	10.1*	4.5*	3.4	5.2*	2.0	NS
IPL (BA40)	L	-36	-36	45	10.1*	7.7*	4.2*	4.7*	2.7*	-3.8 [∇]
	R	39	-36	45	9.1*	4.8*	5.3*	NS	3.9*	NS
SPL (BA7)	L	-30	-51	45	10.0*	13.1*	3.8	9.0*	NS	NS
	R	30	-54	51	12.0*	12.2*	NS	7.8*	3.7*	NS
	L	-21	-57	66	19.4*	5.7*	3.6	4.8*	10.9*	NS
	R	15	-66	60	13.6*	NS	NS	4.0*	8.4*	NS
PostCG (BA7)	L	-3	-51	69	8.8*	NS	NS	NS	7.7*	NS
	R	3	-51	69	10.4*	NS	NS	NS	9.8*	NS
SOG (BA19)	L	-27	-81	27	4.7*	NS	5.5*	NS	NS	NS
	R	33	-81	21	13.2*	NS	5.9*	NS	6.2*	3.6 [∇]
IOG (BA19)	L	-36	-66	-6	6.4*	7.1*	5.4*	4.6*	NS	NS
	R	36	-66	-6	7.4*	5.2*	NS	NS	NS	NS
Thalamus	L	-9	-18	9	8.3*	8.2*	3.4*	NS	NS	3.5 [∇]
	R	3	-21	9	10.1*	8.2*	NS	NS	NS	NS
CER-Declive	L	-33	-66	-21	4.7*	5.5*	5.1*	3.3*	NS	NS
	R	33	-66	-21	8.1*	12.0*	4.2*	7.2*	NS	NS
CER-Vermis	C	-3	-78	-15	10.9*	11.0*	4.5*	5.8*	NS	NS

* Cluster-level corrected $p < 0.001$.

Cluster-level corrected $p < 0.05$.

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Table 2

Cross correlation factors of load responses in the activated networks during WM (shaded up triangle) and VA (open down triangle) tasks. Gray highlights: regions where cross-correlation coefficients were different across tasks.

	IFG	MFG6	MFG9	medFG	FusG	IPL	SPL	PostCG	SOG	IOG	Thalamus	Cerebellum
IFG		0.89	0.94	0.84	0.59	0.76	0.29	0.21	0.56	0.66	0.84	0.57
MFG6	0.73		0.85	0.84	0.53	0.75	0.27	0.35	0.43	0.62	0.76	0.54
MFG9	0.71	0.58		0.92	0.52	0.74	0.11	0.35	0.39	0.62	0.80	0.47
medFG	0.75	0.51	0.79		0.37	0.66	0.15	0.15	0.56	0.48	0.73	0.35
FusG	0.58	0.69	0.60	0.49		0.79	0.66	0.41	0.82	0.96	0.49	0.90
IPL	0.48	0.43	0.59	0.44	0.58		0.53	0.42	0.76	0.86	0.70	0.77
SPL	0.50	0.42	0.72	0.64	0.56	0.47		0.74	0.71	0.62	0.28	0.69
PostCG	0.52	0.52	0.24	0.40	0.51	0.16	0.42		0.53	0.40	0.29	0.58
SOG	0.53	0.48	0.42	0.37	0.73	0.68	0.41	0.35		0.81	0.46	0.78
IOG	0.45	0.50	0.49	0.40	0.90	0.48	0.41	0.29	0.65		0.55	0.90
Thalamus	0.68	0.56	0.56	0.55	0.35	0.36	0.52	0.46	0.28	0.15		0.56
Cerebellum	0.45	0.52	0.49	0.49	0.86	0.52	0.58	0.53	0.68	0.80	0.32	