



Task-related, low-frequency task-residual, and resting state activity in the default mode network brain regions

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The hypothesis of a default mode network (DMN) of brain function is based on observations of task-independent decreases of brain activity during effort as participants are engaged in tasks in contrast to resting. On the other hand, studies also showed that DMN regions activate rather than deactivate in response to task-related events. Thus, does DMN “deactivate” during effort as compared to resting? We hypothesized that, with high-frequency event-related signals removed, the task-residual activities of the DMN would decrease as compared to resting. We addressed this hypothesis with two approaches. First, we examined DMN activities during resting, task residuals, and task conditions in the stop signal task using independent component analysis (ICA). Second, we compared the fractional amplitude of low-frequency fluctuation (fALFF) signals of DMN in resting, task residuals, and task data. In the results of ICA of 76 subjects, the precuneus and posterior cingulate cortex (PCC) showed increased activation during task as compared to resting and task residuals, indicating DMN responses to task events. Precuneus but not the PCC showed decreased activity during task residual as compared to resting. The latter finding was mirrored by fALFF, which is decreased in the precuneus during task residuals, as compared to resting and task. These results suggested that the low-frequency blood oxygen level-dependent signals of the precuneus may represent a useful index of effort during cognitive performance.

Keywords: posterior cingulate cortex, precuneus, default mode network, independent component analysis, spontaneous fluctuation, functional magnetic resonance imaging

INTRODUCTION

There is growing evidence from functional imaging that neural activity during a state of “resting” represents an intrinsic baseline in the default mode network (DMN), including the posterior cingulate cortex (PCC), precuneus, medial prefrontal cortex (MPFC), and inferior parietal lobule (IPL; Gusnard et al., 2001a,b; Raichle et al., 2001; Greicius et al., 2003; Fransson, 2005, 2006; Damoiseaux et al., 2006; Fox and Raichle, 2007; Buckner et al., 2008). During a resting state, these brain regions showed higher regional cerebral blood flow (CBF), local temporal synchrony, and fluctuation amplitude compared to other areas (Zou et al., 2009). The idea of a DMN was supported by two original (Shulman et al., 1997; Mazoyer et al., 2001) and subsequently confirmed by a third (Shannon, 2006) meta-analyses showing that these brain regions routinely decrease activity during task performance, as compared to resting. Thus, this DMN activity is often referred to as task-induced deactivation (TID) because the regions appear deactivated on a cognitive task. For instance, TIDs in several of the default mode regions varied parametrically as a function of task difficulty (McKiernan et al., 2003). Fransson (2006) showed that spontaneous signal fluctuations in the DMN persist and reorganize in response to changes in external work load.

It was hypothesized that these task-independent decreases in CBF are caused by interruption of ongoing processes during

resting state (Shulman et al., 1997; Gusnard et al., 2001a; Mazoyer et al., 2001). On the other hand, some studies suggested that blood oxygen level-dependent (BOLD) signal changes within the DMN could result from respiration- and cardiac-induced variation (Wise et al., 2004; Birn et al., 2006; Shmuel et al., 2007; Chang et al., 2009; van Buuren et al., 2009). Several studies challenged the latter hypothesis by demonstrating a neuronal origin of DMN deactivation. For instance, a recent work employed calibrated fMRI to determine changes in the cerebral metabolic rate of oxygen (CMRO₂) and CBF in the DMN during a cognitive task (Lin et al., 2011). The observations that DMN regions showed a linear CMRO₂/CBF relationship of neuronal activity and CMRO₂/CBF ratios identical to the task-related regions confirmed the neuronal basis of DMN deactivation. The authors identified two modes of DMN deactivation each associated with more and less effort, respectively.

However, the idea of task-independent deactivation of the default brain circuit was wrought with other challenges (Morcom and Fletcher, 2007). Studies showed that behavioral tasks also elicit activity *increases* rather than decreases in the DMN compared to resting or passive fixation (summarized in **Table 1**). For instance, the PCC, anterior cingulate cortex (ACC), and precuneus respond to both pursuit and saccadic eye movement as compared to fixation in an oculomotor task (Berman et al., 1999). Distributed and

Table 1 | Studies showing that tasks elicit activation in the DMN compared to resting or passive fixation.

Study	Regions	Contrast
TASK > RESTING		
Mental navigation task (Ghaem et al., 1997)	PCC, PCu	Mental simulation of routes vs. resting; visual imagery of landmarks vs. resting
Mental imagery task (Knauff et al., 2003)	PCu	Spatial vs. resting; control vs. resting
Verbal working memory task (Osaka et al., 2003)	ACC	Task vs. resting
Go/Nogo task (Wessa et al., 2007)	Left SMG	All go/nogo conditions vs. resting
Memory task (Andreasen et al., 1995)	ACC	Practiced word recall vs. resting; novel word recall vs. resting
Memory task (Andreasen et al., 1999)	ACC	Silent recall of retrieved episodic memory vs. resting
Autobiographical memory task (Fink et al., 1996)	PCC	Autobiographical sentences trail vs. resting
Autobiographical memory task (Markowitsch et al., 2000)	PCC, ACC, PCu	Autobiographic vs. resting; fictitious vs. resting
Sad and happy autobiographical memory task (Markowitsch et al., 2003)	ACC, PCu	Happy vs. resting; sad vs. resting
Pain and attention-demanding task (Davis et al., 1997)	ACC	Pain vs. resting; attention-demanding task vs. resting
Visuo-spatial working memory task (Garavan et al., 2000)	PCC, ACC, PCu, IPL	Task vs. resting
Attention task (Sturm et al., 2006)	ACC, PCu, IPL	Distributed spatial attention vs. resting; focused spatial attention vs. resting
TASK > FIXATION		
Memory and judgment task (Zysset et al., 2002)	MPFC, PCu	Episodic retrieval vs. fixation; evaluative judgment vs. fixation
Memory task (Rothmayr et al., 2007)	PCC, PCu, IPL	Verbally or non-verbally memory delay vs. fixation
Eye movement task (Berman et al., 1999)	PCC, ACC, PCu	Smooth pursuit vs. fixation; visually guided saccades vs. fixation
Attention and motion task (Luks and Simpson, 2004)	ACC, ANG, SMG	Cue period vs. fixation; motion vs. fixation

PCC, posterior cingulate cortex; PCu, precuneus; ACC, anterior cingulate cortex; SMG, supramarginal gyrus; IPL, inferior parietal lobule; MPFC, medial prefrontal cortex; ANG, angular.

focused spatial attention in contrast to resting evoked activation of the ACC, precuneus, and IPL (Sturm et al., 2006).

There is growing evidence that distinguishing task-related and low-frequency BOLD signals may represent a key to disambiguating these seemingly conflicting findings. It has been suggested that baseline or spontaneous neural activity continues during a behavioral task and task-related brain activations represent a combination of the spontaneous activity and responses to stimulus inputs, behavioral outputs, and/or attention (Arfanakis et al., 2000; Fox et al., 2006a; Fair et al., 2007). In particular, Fair et al. (2007) reported that the functional connectivity of low-frequency task-residual signals (with task-elicited signals filtered, please see Methods for details) are similar to resting state. Thus, by removing task-evoked signals, one may recover spontaneous activity of the DMN during a cognitive task. In particular, one can address the possibility whether, after high-frequency signals are removed, DMN deactivate in the task residuals as compared to resting.

Indeed, our recent work showed greater activity in brain regions of the DMN – including the precuneus – during task residuals as compared to resting state in 33 adult individuals (Zhang and Li, 2010). Furthermore, we observed that the fractional amplitude of low-frequency fluctuation (fALFF) of the precuneus is greater during task residual as compared to resting. These findings support a specific role of the precuneus in mediating effort or behavioral engagement.

In the current study, we aimed to replicate and extend these earlier findings in a larger group of participants ($n = 76$). Specifically, we would show that the fALFF and the component activity (as

defined by independent component analysis, ICA) of the DMN regions is decreased during task residuals as compared to resting. In contrast, we would expect greater task-evoked activation in the default brain regions as compared to both resting and task residuals.

MATERIALS AND METHODS

SUBJECTS AND BEHAVIORAL TASKS

Seventy-six healthy adult subjects (41 men, 19–55 years of age, all right-handed) participated in four 10-min sessions of a stop signal task (SST), as described in our previous studies (Chao et al., 2009; Li et al., 2009a,b; Hendrick et al., 2010; Ide and Li, 2011a,b; Zhang and Li, 2012a), and a 10-min resting session during fMRI. All participants were without neurological or axis I psychiatric illnesses and reported no history of head injury or use of illicit substances. In the resting state, they were instructed to relax and stay awake.

In the SST, there were two trial types: “go” and “stop,” randomly intermixed. A small dot appeared on the screen to engage attention at the beginning of a go trial. After a randomized time interval (fore-period) anywhere between 1 and 5 s, the dot turned into a circle, prompting the subjects to quickly press a button. The circle vanished at button press or after 1 s had elapsed, whichever came first, and the trial terminated. A premature button press prior to the appearance of the circle also terminated the trial. Three quarters of all trials were go trials. In a stop trial, an additional “X,” the “stop” signal, appeared after the go signal. The subjects were told to withhold button press upon seeing the stop signal. Likewise, a trial terminated at button press or when 1 s had elapsed

since the appearance of the stop signal. The stop trials constituted the remaining one quarter of the trials. There was an inter-trial-interval of 2 s. The SSD started at 200 ms and varied from one stop trial to the next according to a staircase procedure, increasing and decreasing by 64 ms each after the successful and failed stop trial (Levitt, 1971; De Jong et al., 1990). With the staircase procedure, a “critical” SSD could be computed that represents the time delay required for the subject to succeed in withholding a response half of the time in the stop trials (Levitt, 1971). Subjects were instructed to respond to the go signal quickly while keeping in mind that a stop signal could come up in a small number of trials. Prior to the fMRI study each subject had a practice session outside the scanner. Depending on the actual stimulus timing (e.g., trials varied in fore-period duration) and speed of response, the total number of trials varied slightly across subjects in an experiment. With the staircase procedure we anticipated that the subjects would succeed in withholding their response in approximately half of the stop trials.

IMAGING PROTOCOL

Conventional T1-weighted spin echo sagittal anatomical images were acquired for slice localization using a 3T scanner (Siemens Trio). Anatomical images of the functional slice locations were next obtained with spin echo imaging in the axial plane parallel to the AC–PC line with TR = 300 ms, TE = 2.5 ms, bandwidth = 300 Hz/pixel, flip angle = 60°, field of view = 220 × 220 mm, matrix = 256 × 256, 32 slices with slice thickness = 4 mm and no gap. Functional, BOLD signals were then acquired with a single-shot gradient echo echo-planar imaging (EPI) sequence. Thirty-two axial slices parallel to the AC–PC line covering the whole brain were acquired with TR = 2000 ms, TE = 25 ms, bandwidth = 2004 Hz/pixel, flip angle = 85°, field of view = 220 mm × 220 mm, matrix = 64 × 64, 32 slices with slice thickness = 4 mm and no gap.

IMAGING DATA PREPROCESSING AND GENERAL LINEAR MODELING

Brain imaging data were preprocessed using Statistical Parametric Mapping version 8 (Wellcome Department of Imaging Neuroscience, University College London, UK). Images from the first five TRs at the beginning of each trial were discarded to enable the signal to achieve steady-state equilibrium between RF pulsing and relaxation. Images of each individual subject were first corrected for slice timing and realigned (motion corrected). A mean functional image volume was constructed for each subject for each run from the realigned image volumes. These mean images were normalized to an MNI (Montreal Neurological Institute) EPI template with affine registration followed by non-linear transformation (Friston et al., 1995a; Ashburner and Friston, 1999). The normalization parameters determined for the mean functional volume were then applied to the corresponding functional image volumes for each subject. Finally, images were smoothed with a Gaussian kernel of 8 mm at Full Width at Half Maximum. The data were high-pass filtered (1/128 Hz cutoff) to remove low-frequency signal drifts.

In general linear models (GLM) events of interest were employed as regressors to explain task-related data as described in our previous work (Li et al., 2006, 2007a). Briefly, four main types of trial outcome were distinguished: go success (G), go error (F), stop success (SS), and stop error (SE) trial. A statistical analytical

design was constructed for each individual subject, using the GLM with the onsets of go signal in each of these trial types convolved with a canonical hemodynamic response function (HRF) and with the temporal derivative of the canonical HRF and entered as regressors in the model (Friston et al., 1995b). Additional regressors with the go trial RT and stop trial SSD were also included for parametric modulation. Realignment parameters in all six dimensions were also entered in the model. The data were high-pass filtered (1/128 Hz cutoff) to remove low-frequency signal drifts. Serial autocorrelation was corrected by a first-degree autoregressive or AR(1) model. The GLM estimated the component of variance that could be explained by each of the regressors.

Task-residual time series was obtained by removing task-related activity with the GLM. Based on previous studies that suggested a linear superposition of task activity and spontaneous BOLD fluctuations (Arfanakis et al., 2000; Fox et al., 2006a,b), it was assumed that, if task-induced variance was adequately removed, the remaining residual signal should represent the spontaneous signals (Fair et al., 2007).

GROUP INDEPENDENT COMPONENT ANALYSIS

Multivariate methods based upon ICA have been applied to examine functional connectivity between brain regions both during resting state and task performance (McKeown et al., 1998; Calhoun et al., 2001a,b, 2004, 2008; Jafri et al., 2008). Here we applied three group ICA models to the preprocessed images using the infomax algorithm, each for resting and residual, resting and task, and residual and task data (Bell and Sejnowski, 1995) as implemented in the GIFT (Group ICA of fMRI Toolbox, <http://icatb.sourceforge.net/>, version 2.0) software. We modified the minimum description length criteria to account for spatial correlation to determine the number of independent components (Li et al., 2007b). The three group ICA models were both estimated to have 36 components. Single subject spatial maps were reconstructed, in which the aggregate components and the results from data reduction were used to compute the individual subject components (Calhoun et al., 2001b). The DMN components were selected and the calibrated component image map of each individual subject was computed according to the percent signal change using the original fMRI data as a reference. These calibrated component image maps of all 76 subjects were examined in paired *t* tests for resting vs. task-residual, resting vs. task, and task vs. task residual.

FRACTIONAL AMPLITUDE OF LOW-FREQUENCY FLUCTUATION

To account for power spectrum density of the low-frequency fluctuation, Zang et al. (2007) developed an index – amplitude of low-frequency fluctuation (ALFF) – in which the square root of power spectrum was integrated in a low-frequency range in order to examine the regional intensity of spontaneous BOLD fluctuations. And since the ALFF appeared to be sensitive to the physiological noise, Zou et al. (2008) proposed a fractional amplitude of low-frequency fluctuation (fALFF). We thus carried out the same fALFF analysis on resting, task-residual, and task data as we did in previous study (Zhang and Li, 2010). Briefly, filtered task-residual and resting state time series were transformed into the frequency domain using the fast Fourier transform (FFT). Since the power is proportional to (amplitude)² at a given frequency, the power spectrum obtained by FFT was square rooted to obtain

amplitude. A ratio of the amplitude averaged across 0.009–0.08 Hz to that of the entire frequency range (0–0.25 Hz) was computed at each voxel to obtain the fALFF, creating an amplitude map for the whole brain, which was then normalized: normalized fALFF = (fALFF – global mean fALFF)/standard deviation of global mean.

RESULTS

GROUP INDEPENDENT COMPONENT ANALYSIS

We ran group ICA 20 times using ICASSO (Himberg et al., 2004) and used cluster quality index (I_q) of the default network to assess the repeatability of ICA components. Using paired t tests,

we compared components of the DMN including the precuneus, PCC, and the MPFC. The results showed greater activation in the precuneus during resting as compared to task residuals ($p < 0.05$, corrected for family wise error or FWE of multiple comparisons; **Figure 1C**; **Table 2**) but not when compared to task. The PCC showed less activation during resting as compared to task ($p < 0.05$, FWE corrected; **Figure 1F**; **Table 2**). Both the precuneus and PCC showed greater activity during task as compared to task residual ($p < 0.05$, FWE corrected; **Figure 1I**; **Table 2**).

We extracted the effect size (z scores) of activity of the precuneus and PCC for each of the four SST sessions: for resting vs. residual model (**Figure 2A**), for resting vs. task model (**Figure 2B**),

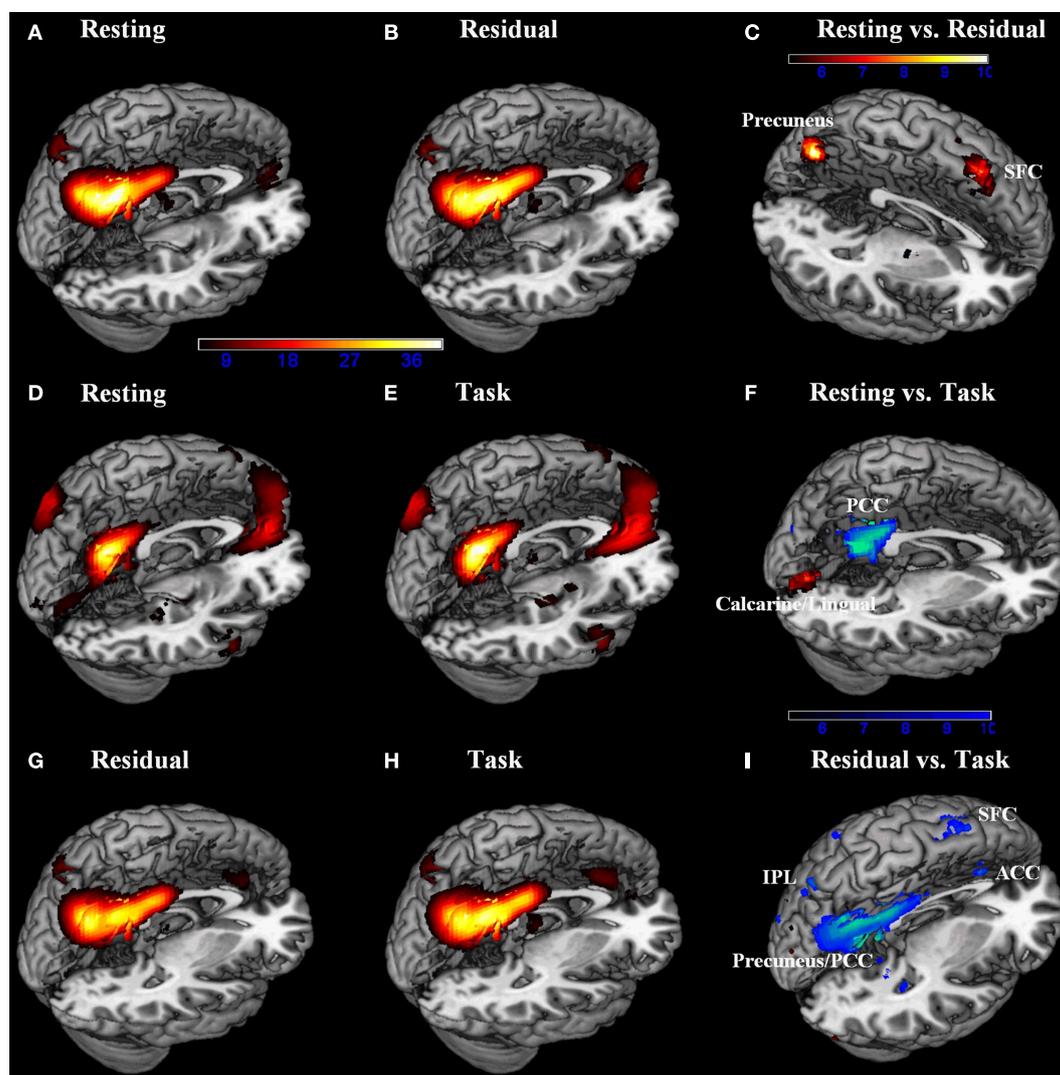


FIGURE 1 | Default network was identified by group independent component analysis each for (A) resting and (B) task-residual data from resting/residual model, for (D) resting and (E) task data from resting/task model, and for (G) task-residual and (H) task data from task-residual/task model ($n = 76$, one sample t test, $p < 0.05$, corrected for FWE; hot: positive). Direct comparisons ($n = 79$, paired t test, $p < 0.05$, corrected for FWE) demonstrated that: (C) the precuneus and bilateral superior frontal cortex (SFC) showed greater

activity during resting compared to task residuals; (F) the posterior cingulate cortex (PCC) showed less activity, while the calcarine/lingual showed greater activity during resting compared to task. (I) the PCC/precuneus, anterior cingulate cortex (ACC), bilateral inferior parietal lobule (IPL), and bilateral SFC showed less activity during task-residual compared to task. Color bars represent voxel t values. Hot: resting > residual, resting > task, or residual > task; Cool: residual > resting, task > resting, or task > residual.

Table 2 | Regional brain activations of default network during resting compared to residual, during resting compared to task, and during residual compared to task.

Cluster size (mm ³)	Voxel <i>t</i> value	MNI coordinate (mm)			Identified region and approximate BA
		<i>x</i>	<i>y</i>	<i>z</i>	
RESTING > RESIDUAL					
3,672	10.15	0	-73	46	Precuneus
3,510	8.62	-15	26	52	Left superior frontal cortex
2,106	7.41	15	23	49	Right superior frontal cortex
RESIDUAL > RESTING					
None					
RESTING > TASK					
2,025	7.58	0	-82	1	Calcarine/lingual
TASK > RESTING					
16,362	12.58	-6	-49	19	Posterior cingulate cortex
RESIDUAL > TASK					
None					
TASK > RESIDUAL					
44,253	10.94	6	-52	13	Precuneus/posterior cingulate cortex
6,237	9.64	-18	-4	52	Left superior frontal cortex
5,535	8.98	21	5	52	Right superior frontal cortex
324	7.27	3	26	31	Anterior cingulate cortex
1,215	7.20	-33	-64	43	Left inferior parietal lobule
486	7.19	39	-55	46	Right inferior parietal lobule

and for residual vs. task model (Figure 2C). Task residuals showed significant lower activity in the precuneus for all sessions compared to resting state (all $p < 0.0001$, paired t test). In contrast, task data showed significant higher activity in the PCC for all sessions compared to resting state (all $p < 0.0001$, paired t test). Across four sessions, task-residual precuneus activity increased across sessions (planned pair-wise comparisons: session 1 < 2, $p = 0.002$; session 2 < 3, $p = 0.3$; session 3 < 4, $p = 0.05$). In contrast, PCC activity during task decreased across the four sessions (planned pair-wise comparisons: session 1 > 2, $p = 0.002$; session 2 > 3, $p = 0.01$; session 3 > 4, $p = 0.06$).

In linear regressions, we correlated the component weight of the precuneus with SST performance measures. The results showed a negative correlation with the median go trial RT ($p = 0.0035$, $r = -0.33$) and a positive correlation with the go trial success (RT < 1 s) rate ($p = 0.0007$, $r = 0.38$). These findings suggest that greater engagement is associated with more cautious responses in the SST (see Discussions).

FRACTIONAL AMPLITUDE OF LOW-FREQUENCY FLUCTUATION

In region of interest analyses, the precuneus showed greater fALFF during resting compared to task residuals ($p < 0.05$, two-tailed paired t test), but less fALFF during resting compared to task (Figure 3). In contrast, the PCC showed less fALFF during resting compared to either task residual or task (all $p < 0.001$).

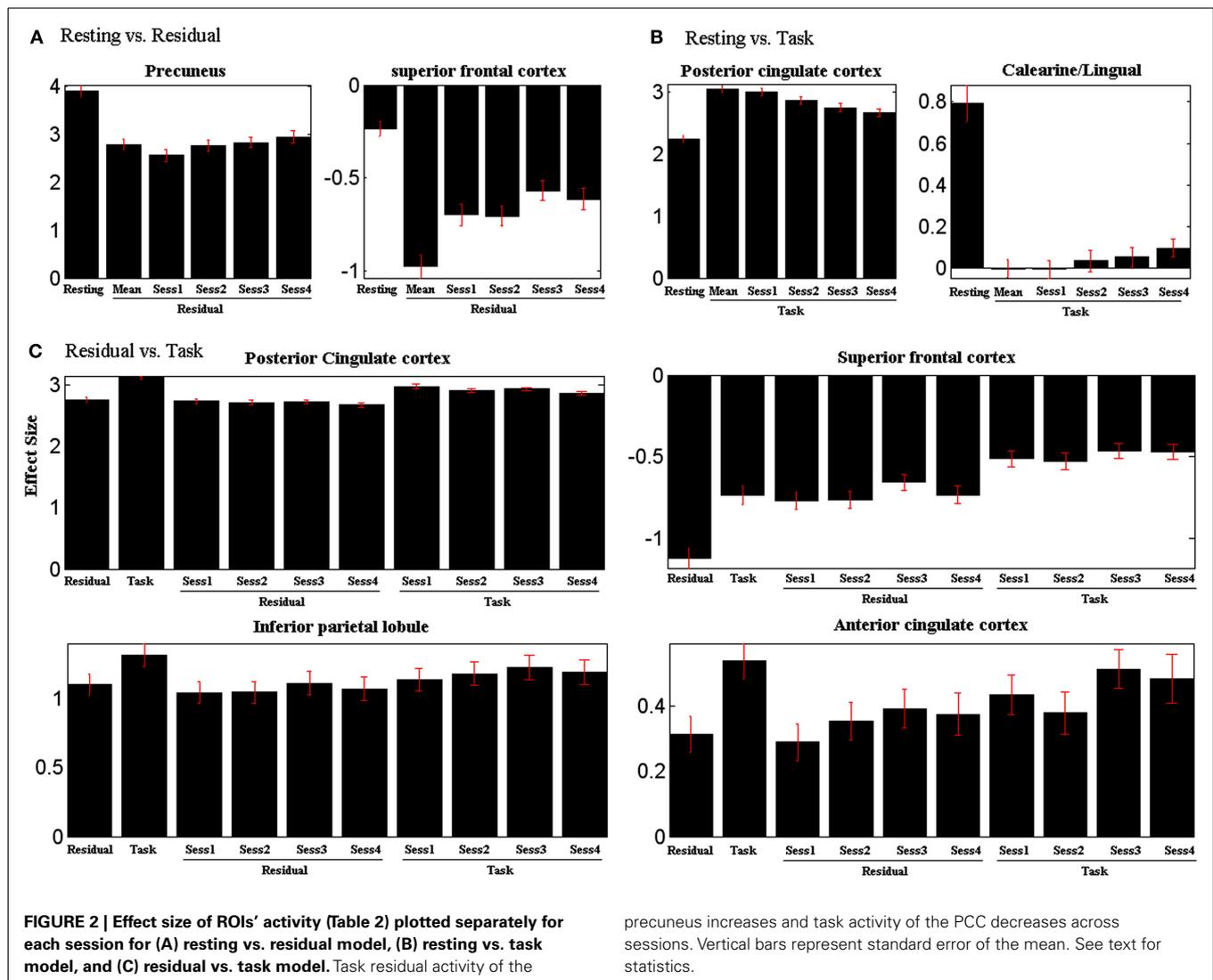
DISCUSSION

TASK-RESIDUAL LOW-FREQUENCY ACTIVITY OF THE PRECUNEUS AND MENTAL EFFORT

The current findings from a large data set confirmed our hypothesis that task-residual low-frequency activity in the precuneus

represents a neural surrogate of task engagement (Zhang and Li, 2010). The more subjects were engaged in the task, the less low-frequency activity was observed in the precuneus. The current results support the activity of task residuals of the DMN as a neural analog of effort. Indexed by the activity effect size from ICA and the fALFF, the dorsal precuneus decreased in activity during task residuals as compared to resting. The precuneus increased activity during the task, as compared to resting. Only in task residuals, where task-related signals are removed, can we observe decreased activity in the precuneus, as compared to resting. This result is consistent with many previous findings (Gusnard et al., 2001a; McKiernan et al., 2003, 2006; Fransson, 2006). For instance, Fransson (2006) showed that spontaneous intrinsic activity in the DMN is attenuated during performance of a working memory task compared to resting. More recently, a study of traumatic brain injury (TBI) patients showed that sustained attention impairments were associated with an increase in DMN activity, particularly within the precuneus and PCC (Bonnelle et al., 2011). Another work showed that deactivation of the DMN regions including the precuneus is inversely associated with the directional coherence of the moving dots, associating DMN deactivation with effort in visual motion discrimination (Singh and Fawcett, 2008).

Evidence is accumulating to support the idea that the low-frequency spontaneous signals are not random noise but functionally organized activity that occurs both during resting and during exposure to stimuli and cognitive challenges (Raichle et al., 2001; Greicius et al., 2003; Fox et al., 2006b; Hampson et al., 2006; Fair et al., 2007; Fox and Raichle, 2007; Raichle and Snyder, 2007). Our findings confirmed this view in that activities in the PCC, precuneus, MPFC, and IPC are organized and persists in the task-residual and task data as a network (Raichle et al., 2001;



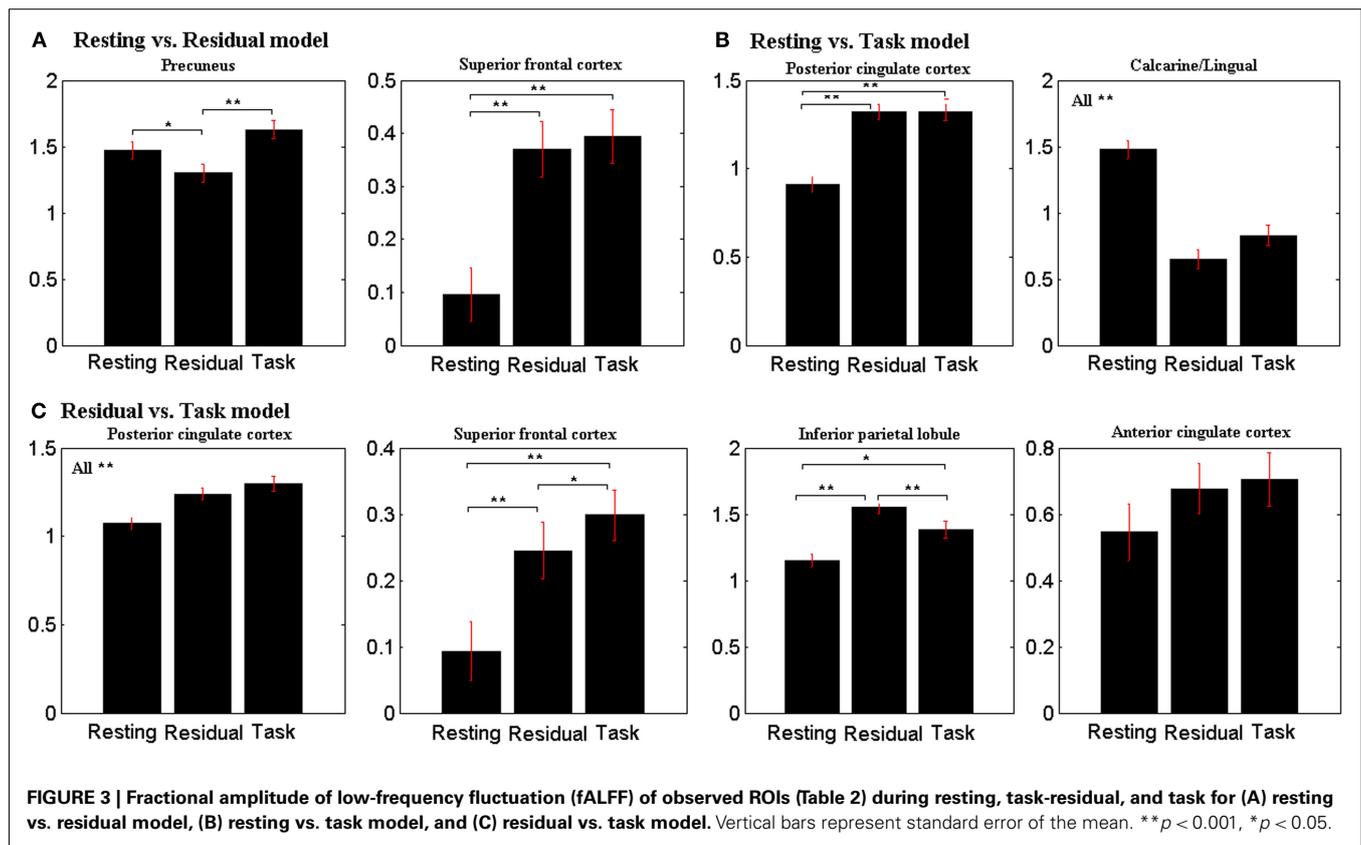
Greicius et al., 2003; Fransson, 2005, 2006; Hampson et al., 2006; Fox and Raichle, 2007; Buckner et al., 2008). Significant DMN activities remained with the task-residual data, with the precuneus showing decreased activity as compared to both resting and task condition. Thus, default network processes can be carried on in parallel with task performance, during which subjects intermittently activate this network in response to task events (Hampson et al., 2006; Fox and Raichle, 2007).

The DMN is hypothesized to play a role in monitoring the external environment. The critical difference, between task-directed conditions that suspend activity and passive conditions that augment activity within the DMN, is the form of their attentional focus on the external world (Shulman et al., 1997; Gusnard et al., 2001a; Mazoyer et al., 2001; Gilbert et al., 2007; Hahn et al., 2007). When non-self-referential goal-directed processes are to be performed, the default processes are interrupted, reflecting a necessary reduction in resources devoted to general information gathering and evaluation. Therefore, the more engagement in a goal-directed task, the less activity decrease can be identified within the default network. Interestingly, the low-frequency signals of the precuneus

increased across the four sequential sessions, suggesting that participants gradually adapt engage less mental effort to the task. In contrast, task-related activations in the PCC showed the opposite pattern of responses (see below). These results suggest an interaction of effort- and task-related activations of the DMN.

DMN RESPONSES TO BOTH TASK EVENTS AND EFFORT

The default brain regions could activate rather than deactivate in response to task-related events. We observed greater activation in the PCC during task as compared to resting state, consistent with many earlier findings obtained with different behavioral paradigms (Fink et al., 1996; Ghaem et al., 1997; Berman et al., 1999; Garavan et al., 2000; Markowitsch et al., 2000). A study showed that working memory performance was positively associated with functional connectivity between the PCC and MPFC not only during the task but also at rest (Hampson et al., 2006). The authors suggested that these regions may serve multiple roles rather than only disengage during cognitive tasks, a view that have been affirmed by other studies (Gilbert et al., 2007; Leech et al., 2011, 2012; Pearson et al., 2011).



Notably, the observed PCC activation during task as compared to resting in our study is within the dorsal PCC. These results are consistent with two recent studies showing a dissociated pattern of activations between dorsal and ventral PCC in an attentionally demanding task (Leech et al., 2011, 2012). The dorsal PCC showed functional connectivity with both the DMN and the task-related network, while the ventral PCC showed connectivity only with the DMN. Furthermore, the PCC was suggested as an important connectivity hub by both functional and structural studies (Hagmann et al., 2008; Tomasi and Volkow, 2011). Tomasi and Volkow (2011) proposed that the PCC performs multimodal information transfer and integration, which is essential for processing spontaneous thoughts and internal awareness. Hagmann et al. (2008) investigated structural connectivity by diffusion tensor imaging, and identified a structural core comprising posterior medial and parietal cortical regions that are densely interconnected and topologically central. Taken together, these results suggest that the dorsal PCC may play an active role in the regulation of cognitive functioning besides default network activity.

Perhaps because of the mixture of responses to task-related events and effort, many previous studies reported seemingly inconsistent findings on DMN activation during cognitive performance. For instance, the activity of the default regions, such as the PCC, decreased along with the increased memory load (McKiernan et al., 2003). However, the authors observed an opposite pattern for the precuneus. A possible explanation might be that the precuneus was activated by the task while behavioral

engagement caused deactivation at the same time. Such task-evoked precuneus activity compared to resting or fixation condition have been widely reported (Garavan et al., 2000; Markowitsch et al., 2000; Zysset et al., 2002; Rothmayr et al., 2007). This contrasting pattern of responses of the PCC and precuneus to the working memory task appears to be the opposite of our current findings. Thus, whether a DMN region activates more to task-related events or deactivates more to behavioral engagement may be task-specific. This issue warrants investigation in the future.

CONCLUSION AND LIMITATION

Thus, task engagement will attenuate spontaneous activity in the DMN while task-related events may increase its activity. The observed signal changes are due to a simple superposition of the spontaneous and task-evoked activity (Fox and Raichle, 2007). Consistent with this hypothesis, our findings suggest that task-residual plays an important role in task engagement. Identification of task residual signals helps elucidate changes in spontaneous activity of the DMN, which may represent a neural signature of effort during cognitive performance.

An important issue remains to be resolved. The precuneus that we identified as the neural surrogate of effort is within the dorsal part of the medial posterior parietal cortex. Our recent study of connectivity mapping showed that the ventral but not the dorsal precuneus is within the default network (Zhang and Li, 2012b, see also Buckner et al., 2008). In contrast, dorsal precuneus is connected to brain regions in control of attention and mental

imagery. A recent study supported this functional distinction by showing decreased regional CBF in the posterior cingulate gyrus, medial frontal cortex, and ventral but not dorsal precuneus, in participants performing a spatial working memory task, as compared to rest (Pfefferbaum et al., 2011). Thus, although both the dorsal and ventral precuneus appear to be involved in behavioral engagement to an external task, their specific roles remained to be specified.

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