

## Age differences in the neural correlates of distraction regulation: A network interaction approach



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### ABSTRACT

Older adults show decrements in the ability to ignore or suppress distraction relative to younger adults. However, age differences in the neural correlates of distraction control and the role of large-scale network interaction in regulating distractors are scarcely examined. In the current study, we investigated age differences in how the anticorrelation between an externally oriented dorsal attention network (DAN) and an internally focused default mode network (DMN) is related to inhibiting distractors presented during a 1-back working memory task. For both young and older adults, the extent of DAN-DMN anticorrelation predicted reduced distractibility. Activation in a common set of frontal and insular control regions during the task was, however, associated with opposite patterns of network interaction and distractibility in the age groups. For older adults, recruitment of these regions was associated with greater DAN-DMN anticorrelation and less distractibility (better performance). For younger adults, it was associated with decreased DAN-DMN anticorrelation and more distractibility (worse performance). Our findings demonstrate the age-dependent relationship between DAN-DMN interaction patterns and engagement of control regions during an externally oriented distraction control task. This suggests that engagement of those regions may play a compensatory role for older adults but may be indicative of less efficient neural control mechanisms in younger adults.

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### Introduction

Paying attention to one thing often requires successfully ignoring others. This ability, known as distraction control, contributes to many cognitive skills (such as working memory, task-switching, and recall) and is known to vary between individuals and across the lifespan (e.g., Hasher and Zacks, 1988; Kane and Engle, 2003). Behavioral and neuroimaging studies have demonstrated that older adults, on average, show reduced distraction control and process more distractors relative to younger adults (e.g., Campbell et al., 2012; Gazzaley et al., 2005; Hasher et al., 1999; Rowe et al., 2006; Schmitz et al., 2010). Age differences in the neural correlates of distraction control in the context of large-scale network interactions are, however, rarely studied.

Distraction control and selective attention are commonly associated with activity in a set of frontal and parietal control regions. These include the dorsolateral prefrontal cortex (dlPFC), frontal eye fields (FEF), intraparietal sulcus (IPS), and superior parietal lobule (SPL; e.g., Corbetta and Shulman, 2002; Kanai et al., 2011; Kelley et al.,

2008; Minamoto et al., 2012). These regions are typically correlated during task performance and at rest and form an externally oriented dorsal attention network (DAN) involved in the top-down selection of external relevant stimuli based on task goals (Corbetta and Shulman, 2002; Corbetta et al., 2008; Vincent et al., 2008). Another network implicated in distractibility is the default mode network (DMN; Raichle et al., 2001). The DMN, which includes the medial prefrontal cortex (mPFC), posterior cingulate cortex (pCC), and the posterior extent of the inferior parietal lobule (pIPL), is involved in internally focused cognitive processes, such as autobiographical memory and imagining the future (e.g., Andrews-Hanna et al., 2014; Rugg and Vilberg, 2013; Schacter et al., 2007). This latter network is typically deactivated during tasks making demands on externally-driven attention, and its lack of suppression is associated with distractibility and attentional lapses (e.g., Chadick et al., 2014; Weissman et al., 2006).

The DAN and DMN have an intrinsic competitive relationship, with activity in one usually suppressing the other (e.g., Fox et al., 2005; Keller et al., 2013; McKiernan et al., 2003 Spreng et al., 2010). The DMN is suppressed during externally-oriented tasks such as working memory (Anticevic et al., 2010; Anticevic et al., 2012b), visual search (Shulman et al., 2007), and memory encoding tasks (Daselaar et al., 2004; Otten and Rugg, 2001). Greater DMN suppression is associated

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with enhanced performance on all these tasks. Additionally, the extent of the DAN-DMN anticorrelation at rest predicts performance on attention (Kelly et al., 2008), working memory (Keller et al., 2015; Sala-Llonch et al., 2012), and fluid intelligence (Cole, Yarkoni, Repovš, Anticevic, & Braver, 2012) tasks, suggesting that the networks' intrinsic functional antagonism supports a range of cognitive functions.

Several studies have demonstrated that older adults show reduced suppression of the DMN relative to younger adults. Older adults generally show greater DMN activation during the performance of externally oriented verbal and nonverbal spatial tasks, and fail to modulate the level of DMN activity on the basis of task demand to the same extent as younger adults (e.g., Grady et al., 2006; Lustig et al., 2003; Miller et al., 2008; Park et al., 2010; Persson et al., 2007; Prakash et al., 2012). Additionally, older adults show greater coupling between the DMN and control regions during external tasks (Spreng and Schacter, 2012; Turner and Spreng, 2015), suggesting the possibility that the DMN interferes with older adults' cognitive performance.

This lack of DMN regulation may be mediated by diminished top-down signals from regions generally involved in cognitive control, such as the anterior insula (aINS), anterior cingulate cortex (ACC), and lateral frontal areas, that modulate activity in DMN regions in accordance with task demands (e.g., Chen et al., 2013; Wen et al., 2013). Although older adults show reduced activation in some of these control regions during distraction control tasks (e.g., Anderson et al., 2014; Campbell et al., 2012), and age-related increased DMN activation has long been suggested to be a source of vulnerability to distraction (e.g., Grady et al., 2006), the anticorrelation between control and DMN regions has never been investigated in relation to age differences in distractibility. That is, although DMN regions are thought to play a role in age differences in distractibility (e.g., Chadick et al., 2014; Stevens et al., 2008), the specific control areas involved in suppressing those regions, or driving their anticorrelation with the DAN during distraction regulation, are relatively unknown. Furthermore, the extent to which recruitment of those areas is related to successful DAN-DMN decoupling and inhibition of distractors in younger versus older adults has not been examined.

In the current study, we investigated the neural regions associated with the extent of DAN-DMN anticorrelation during a distraction control task, and we examined the relationship between recruitment of those regions and distractibility within groups of older and younger adults. Participants were scanned as they performed a 1-back task on pictures with superimposed distractor words. Subsequent implicit memory for the words (priming), which served as an index of distractibility, was tested using a fragment completion task. Thus, our measure of distractibility was based on processing of distracting information during the 1-back working memory task, as well as sustained access to that information over a brief delay period. Measuring access to previous distractors is a reliable measure of distraction control and shows typical age differences in distractibility (e.g., Amer and Hasher, 2014; Biss et al., 2013a; Rowe et al., 2006). We identified brain regions where increased activity during the 1-back task was simultaneously associated with the extent of the DAN-DMN anticorrelation and distractibility.

To preface our results, we found that greater recruitment of control areas typically involved in DMN regulation, such as the aINS, ACC, and lateral frontal regions (e.g., Chen et al., 2013; Wen et al., 2013), was associated with increased DAN-DMN anticorrelation and enhanced distraction regulation in older adults. For younger adults, however, activation in the same areas was associated with decreased DAN-DMN anticorrelation and reduced distraction regulation. Our results suggest that recruitment of those regions played a compensatory role in older adults (e.g., Grady, 2012; Reuter-Lorenz and Park, 2014) and facilitated the anticorrelation between the DAN and DMN, which was subsequently associated with reduced access to distraction. Conversely, increased activation of the same control areas in younger adults related to worse cognitive performance, suggesting that recruitment of the same control regions in younger adults, at least at this level of demand, reflects less

efficient neural functioning (e.g., Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014; Rypma and D'Esposito, 2000; Smith et al., 2001).

## Materials and methods

### Participants

Participants were 16 younger (18–30 years;  $M = 23.69$ ,  $SD = 4.41$ ; 7 males) and 16 older (60–82 years;  $M = 70.88$ ,  $SD = 7.58$ ; 4 males) adults. Data from the participants were reported in two previous studies examining age differences in mean activity during distraction control (Anderson et al., 2014; Campbell et al., 2012). All participants were right handed, had normal or corrected to normal vision based on a visual acuity test conducted before the scanning session, and had no history of any psychiatric or neurological disorder that might compromise cognitive function. Older adults were cognitively intact, as indicated by their scores on the Mini Mental State Exam (26–30;  $M = 28.50$ ,  $SD = 1.72$ ). The two groups were matched on years of education (Younger adults:  $M = 15.94$ ,  $SD = 3.94$ ; Older adults:  $M = 15.94$ ,  $SD = 2.08$ ), and scores on the Shipley Vocabulary test (Younger adults:  $M = 33.64$ ,  $SD = 3.46$ ; Older adults:  $M = 34.66$ ,  $SD = 3.75$ ; Shipley, 1946),  $ps > 0.4$ . Data from 1 younger adult were eliminated for noticing a connection between the 1-back and fragment completion tasks (see below for more details).

### Experimental design

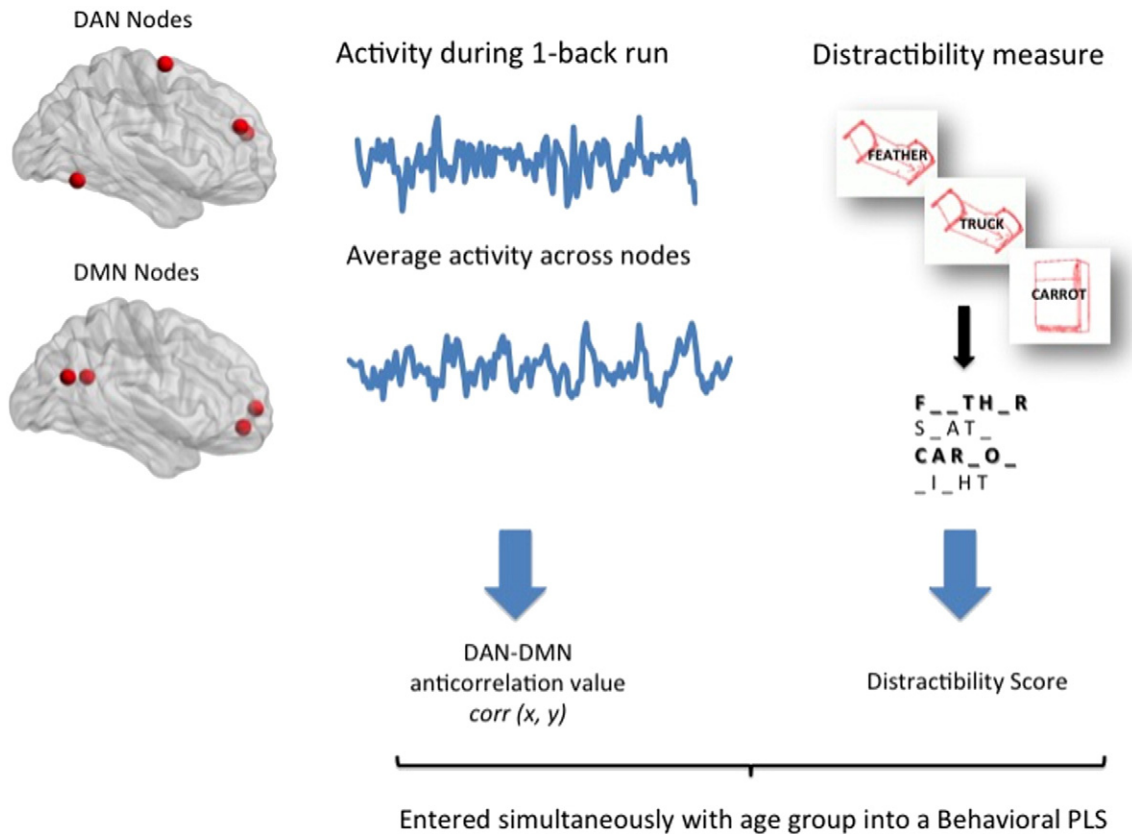
Participants were scanned as they performed a 1-back task on pictures with superimposed irrelevant words/nonwords that they were instructed to ignore. Following a 7-min nonverbal filled delay, implicit memory for the unattended words from the 1-back task was tested using a word-fragment completion task (unscanned). Additional tasks that were not analyzed in the current study were administered in the scanner, as outlined in Anderson et al. (2014) and Campbell et al. (2012).

For the 1-back task, participants viewed a series of superimposed picture and letter stimuli (words and nonwords), with the pictures shown in red and the letters shown in black. Each stimulus pair was shown for 1000 ms, followed by a blank screen for 500 ms. Participants were asked to attend to the pictures and to press a response key whenever the same picture appeared twice in a row. They were told to ignore the letter stimuli, as attention toward these stimuli would only worsen target task performance. One-back targets occurred every six trials on average and never coincided with targets for the word-fragment task. A block design was used, with the letter stimuli divided into word and nonword blocks. Two lists with different superimposed irrelevant words were counterbalanced across participants. The 1-back task began with 10 s of fixation, followed by eight task blocks of 24 s each, interleaved with eight fixation blocks of 14 s each. Each task block

**Table 1**  
Nodes selected from the DAN and DMN.

Region	Hem	X (mm)	Y (mm)	Z (mm)
<i>DAN nodes</i>				
Frontal eye field	R	28	−4	64
Dorsolateral prefrontal cortex	L	−20	48	20
	R	24	44	24
Middle temporal motion complex	R	44	−60	−16
<i>DMN nodes</i>				
Anterior medial prefrontal cortex	L	−4	56	4
Ventral medial prefrontal cortex	L	−4	48	−8
Posterior inferior parietal lobule	L	−56	−64	20
	R	48	−64	24
Posterior cingulate cortex	L	−4	−52	24

Note: Hem = hemisphere; R = right; L = left.



**Fig. 1.** Analysis summary. DAN-DMN anticorrelation values were calculated by correlating average activity of the nodes from each network during the 1-back run. Distractibility scores were calculated by measuring priming for unattended words presented during the “ignore words” condition of the 1-back task. These variables were entered (along with age group) into a behavioral partial least squares analysis (PLS) to identify the brain regions that are associated with the extent of DAN-DMN anticorrelation and distractibility in younger and older adults.

contained 16 trials of the same condition and thus, there were 64 trials per condition. Pictures were taken from [Snodgrass and Vanderwart \(1980\)](#) and superimposed with either random consonant strings or words (including 10 words that would later serve as targets on a word-fragment-completion task).

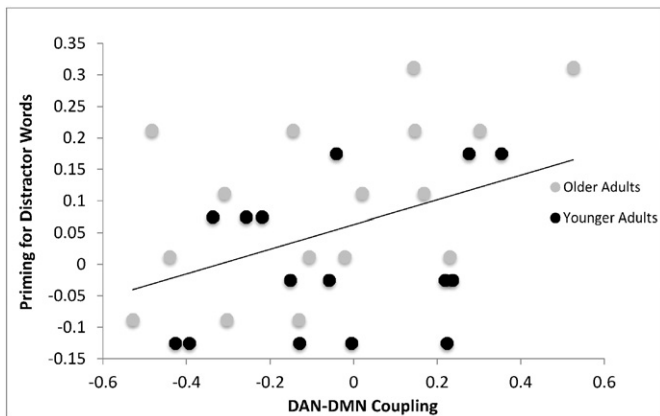
Following a 7-min nonverbal filled interval, memory for unattended superimposed words (i.e., the consequence of distractibility during the 1-back task) was tested using word-fragment completion. The test included 30 word fragments: 10 were target fragments that could be solved with words seen on the preceding 1-back task, 10 were control

fragments which participants from another counterbalance condition would have seen, and 10 were easily solved fragments that served to maintain morale and to obscure the connection between the test and previous input task. Each fragment was shown in the center of the screen for 3000 ms and participants were told to respond aloud with the first solution that came to mind. All fragments had multiple solutions in the language, but only one in the experiment. Separate baseline word-fragment completion rates (i.e., the proportion of solved fragments from the unseen list) were determined for each age group, and priming was calculated as the difference between each individual's target word fragment completion rate and the corresponding group average baseline rate, as is typical in the priming literature. Following the task, participants were asked if they noticed a connection between the 1-back and word fragment tasks. Only 1 younger adult was aware of the connection between the tasks.

#### *fMRI data acquisition and analysis*

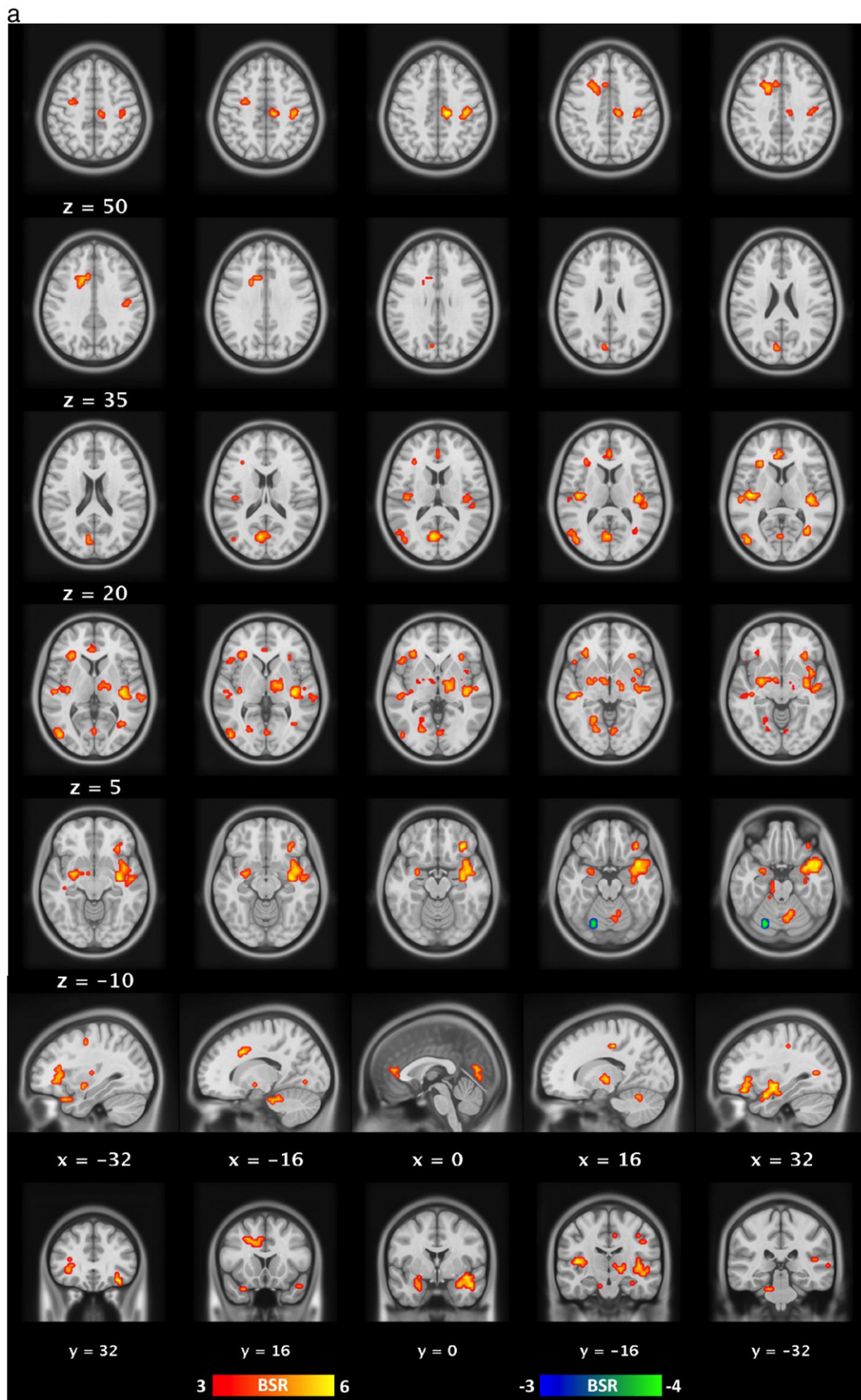
Participants were scanned using a Siemens Trio 3T scanner (Erlangen, Germany). Anatomical scans were acquired with a three-dimensional magnetization-prepared rapid acquisition with gradient echo (MP-RAGE) sequence (repetition time (TR) = 2 s, echo time (TE) = 2.63 ms, field of view (FOV) = 25.6 cm<sup>2</sup>, 256 × 256 matrix, 160 slices of 1-mm thickness). Functional runs were acquired with an echo planar imaging (EPI) sequence, with 157 volumes for the 1-back run (TR = 2 s, TE = 30 ms, flip angle = 70°, FOV = 20 cm<sup>2</sup>, 64 × 64 matrix, 30 slices of 5-mm thickness, no gap). Measures of pulse and respiration were obtained during the scan.

Preprocessing of the image data was performed with analysis of functional neuroimages ([Cox, 1996](#)). This included physiological motion correction, rigid motion correction, spatial normalization to Montreal



**Fig. 2.** Correlation between the extent of DAN-DMN coupling and proportion priming for distractor words presented during the 1-back task. Greater DAN-DMN coupling (or reduced anticorrelation) was associated with more priming for distractors across both age groups.





**Fig. 3.** Behavioral PLS analysis showing the brain pattern during the 1-back run associated with DAN-DMN anticorrelation and priming for unattended words (distractibility). The pattern in (a), which includes regions such as the bilateral inferior and left middle frontal gyri and ACC, is associated with greater DAN-DMN anticorrelation (or less coupling) and less distractibility in older adults, but is associated with the opposite pattern in younger adults (as shown in the scatterplots in b). The brain pattern is displayed using *Mango* (Research Imaging Institute, UTHSCSA).

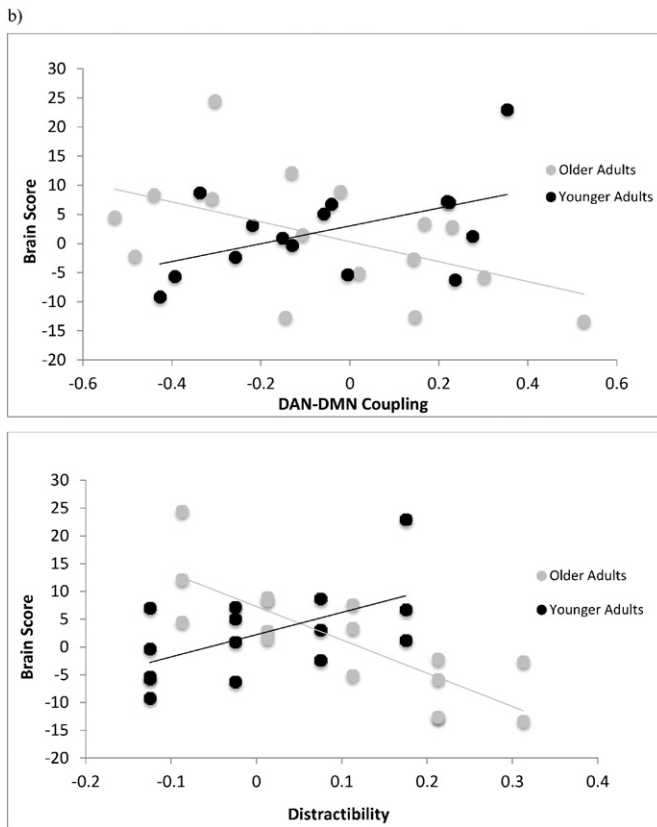


Fig. 3 (continued).

Neurological Institute (MNI) space, and smoothing with an 8-mm Gaussian filter (the final voxel size was  $4 \times 4 \times 4$  mm). We also regressed out the white matter, cerebral spinal fluid, vasculature, and motion–time series from each voxel–time series (Campbell et al., 2013; Grady et al., 2010) and did not analyze the first 2 TRs from each block. Given that standard motion correction procedures do not eliminate the impact of motion on brain activity and connectivity measures, (e.g., Power et al., 2012), we followed a motion-scrubbing procedure described in Campbell et al. (2013). Briefly, this procedure uses a multivariate technique to identify outliers in both the motion-parameter estimates and fMRI signal intensity. Where such outliers co-occurred (never > 5% of the total volumes), we removed the fMRI volumes and replaced them with adjacent values interpolated with cubic splines. As reported by Campbell et al. (2013), this method has the advantage of suppressing spikes, yet keeping the length of the time course intact across subjects.

The image data were analyzed with partial least squares (PLS; for a detailed tutorial and review of PLS, see Krishnan et al., 2011; McIntosh et al., 1996; McIntosh et al., 2004), a multivariate analysis technique that identifies whole-brain patterns of activity associated with task conditions (task-PLS) or behavioral variables (behavioral-PLS). This method is similar to principal component analysis (PCA), in that it identifies a set of principal components, or “latent variables” (LVs), which optimally capture the covariance between two sets of measurements (Friston et al., 1993). PLS uses singular value decomposition in a data-driven approach to reduce the complexity of the dataset into orthogonal LVs that attempt to explain the maximum amount of covariance between the task conditions or behavioral variables and the blood-oxygen level dependent (BOLD) signal. Behavioral PLS was used in the current study to identify the brain regions during the 1-back task where increased BOLD signal was associated with the extent of DAN-DMN anticorrelation and distractibility in younger and older adults.

For every LV in PLS, each brain voxel has a weight, known as a salience, indicating how strongly that voxel contributes to the LV overall. The significance of each LV as a whole was determined with a permutation test (McIntosh et al., 1996), using 500 permutations. In addition, the reliability of each voxel's contribution to a particular LV was tested by submitting all saliences to a bootstrap estimation of the standard errors (SEs; Efron, 1981), using 500 bootstraps. Peak voxels with a salience/SE ratio  $\geq 3.0$  ( $p < 0.001$ ) are considered to be reliable (Sampson et al., 1989). Hence, this step was included to threshold the identified brain pattern for each LV. Clusters containing at least 5 reliable contiguous voxels were extracted, with a local maximum defined as the voxel with a salience/SE ratio higher than any other voxel in a 2-cm cube centered on that voxel (the minimum distance between peaks was 10 mm). Coordinates of these locations are reported in MNI standard coordinate space (Mazziotta et al., 2001). Because the extraction of the LVs and the corresponding brain images is done in a single step (i.e., the analysis can be considered as “one model”), no correction for multiple comparisons is required, as these corrections are applied when there are multiple statistical tests across voxels.

To obtain summary measures of each participant's expression of the LV spatial pattern, we calculated “brain scores” by multiplying each voxel's salience by the BOLD signal in the voxel, and summing over all brain voxels for each participant. These brain scores were used to examine the correlation between each participant's expression of the spatial pattern and the extent of DAN-DMN anticorrelation and distractibility.

#### DAN-DMN anticorrelation

A DAN-DMN anticorrelation score was calculated for each participant during the entire 1-back task run. A task-based PLS analysis was first used to identify areas in both age groups that showed increased or decreased activity during the task relative to fixation (see Anderson et al., 2014; Campbell et al., 2012 for more details). Then, based on previous work (Spreng et al., 2013), we selected active regions during the task that corresponded to the DAN and suppressed regions that corresponded to the DMN and used those regions as our nodes (see Table 1). To find the coordinates to use for our nodes, we applied anatomical masks of all our regions of interest from the AAL Atlas (Tzourio-Mazoyer et al., 2002) and determined the peak voxel within each region. Then, for each participant, we averaged activity across all nodes within each of the two networks for each volume in the run and correlated the average activity between the two networks to obtain a DAN-DMN anticorrelation score, which was converted into a Fisher's  $z$  score for all subsequent analyses. Finally, the DAN-DMN anticorrelation score was entered into a behavioral PLS, along with distractor memory scores and age group, to assess the brain regions during the “ignore words” condition that were associated with both distractibility and the extent of the two networks' antagonistic relationship in younger and older adults (for a summary, see Fig. 1). Note that we were interested in brain regions associated with distractibility and the network anticorrelation during the “ignore words” condition, in particular, because our behavioral measure of distractibility was calculated by measuring implicit memory for words seen during that condition.

## Results

### Behavioral results

A  $2 \times 2$  mixed analysis of variance (ANOVA) on accuracy on the 1-back task, with Age Group as a between-subjects variable and Condition (“ignore words” vs. “ignore non-words”) as a within-subjects variable, showed main effects of Condition  $F(1, 28) = 14.39$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.34$ , and Group  $F(1, 28) = 18.03$ ,  $p < 0.0001$ ,  $\eta_p^2 = 0.39$ , which were qualified by a significant Group  $\times$  Condition interaction,  $F(1, 28) = 13.32$ ,  $p < 0.005$ ,  $\eta_p^2 = 0.32$ . For younger adults, accuracy was near ceiling on the “ignore words” ( $M = 0.99$ ,  $SD = 0.03$ ) and “ignore non-

**Table 2**

Brain areas showing a correlation with the extent of DAN-DMN anticorrelation and distractibility during the 1-back task run. Regions with a positive BSR were associated with a greater DAN-DMN anticorrelation and less distractibility in older adults but reduced anticorrelation and greater distractibility in younger adults. Regions with a negative BSR were associated with the opposite pattern.

Region	BA	Hem	X (mm)	Y (mm)	Z (mm)	BSR
<i>Positive BSR</i>						
Middle frontal gyrus	6	L	−32	−8	48	4.02
Inferior frontal gyrus	47	L	−32	20	−28	4.61
	47	R	32	32	−16	6.13
	45	L	−48	24	0	3.67
Anterior cingulate cortex	24	L	−8	36	8	4.41
Dorsal cingulate cortex	32	L	−16	12	36	5.90
	24	L	−20	8	40	4.65
Cingulate gyrus	31	R	12	−24	44	7.35
Dorsal anterior insula	13	L	−28	28	8	4.72
Dorsal insula	13	L	−44	−16	8	5.92
Postcentral gyrus	3	R	40	−20	44	4.51
Putamen		R	36	−12	−12	6.13
		R	36	−20	0	5.60
		L	−28	−4	−8	4.59
Superior temporal gyrus	22	L	−48	−24	−4	4.37
	22	R	64	−28	4	4.13
Parahippocampus	19	L	−20	−56	−4	3.36
Cuneus	30	L	−8	−72	16	5.64
Inferior occipital gyrus	18	L	−48	−80	4	4.89
Lingual gyrus	19	L	−24	−72	0	4.94
	19	R	36	−64	8	4.49
Thalamus		R	16	−16	0	4.47
Hypothalamus		L	−8	−4	−8	4.29
Cerebellum		L	−12	−28	−24	4.35
		R	12	−60	−24	5.04
<i>Negative BSR</i>						
Cerebellum		L	−24	−72	−24	−4.44

Note: BA = Brodmann area; BSR = bootstrap ratio.

words" ( $M = 0.99$ ,  $SD = 0.02$ ) conditions, and did not differ between the conditions,  $p > 0.7$ . Older adults, on the other hand, showed higher accuracy on the "ignore nonwords" ( $M = 0.99$ ,  $SD = 0.04$ ) relative to the "ignore words" ( $M = 0.84$ ,  $SD = 0.14$ ) condition,  $t(14) = 3.86$ ,  $p < 0.005$ ,  $d = 1.43$  (data missing from 1 participant), suggesting that their performance was more disrupted by the presence of meaningful relative to meaningless distractors, consistent with previous reports (e.g., Biss et al., 2013b; Connelly et al., 1991).

The two groups showed no significant difference in the proportion of baseline fragments correctly solved on the word-fragment completion task (Younger adults:  $M = 0.12$ ,  $SD = 0.13$ ; Older Adults:  $M = 0.09$ ,  $SD = 0.1$ ),  $p > 0.4$ . Consistent with previous studies (e.g., Rowe et al., 2006), older ( $M = 0.10$ ,  $SD = 0.14$ ),  $t(15) = 2.94$ ,  $p < 0.05$ ,  $d = 0.71$ , but not younger ( $M = 0.002$ ,  $SD = 0.12$ ),  $p > 0.9$ , adults showed reliable priming for previously presented distractor words, and the group difference in priming was significant,  $t(29) = 2.16$ ,  $p < 0.05$ ,  $d = 0.80$ .

### fMRI results

Prior to conducting the PLS analysis, we tested the association between the degree of DAN-DMN anticorrelation and priming for distractor words (i.e., distractibility). Across both age groups, the degree of DAN-DMN anticorrelation was associated with distractibility,  $r = 0.40$ , 95% CI [0.05, 0.70] (the 95% CIs of all correlations reported are based on 500 bootstrap samples). The effect remained significant,  $r = 0.44$ , 95% CI [0.14, 0.70], when age group was included as a covariate. When analyzed separately, both groups showed an association in the same direction, but only the older group showed a significant effect ( $r = 0.53$ ; young:  $r = 0.31$ ). The weaker effect in younger adults, though in the expected direction, failed to reach significance due to our modest sample size. Thus, consistent with previous reports

(e.g., Sala-Llonch et al., 2012), increased DAN-DMN anticorrelation was generally associated with better performance (less distractibility in this case; Fig. 2). It is important to note that both age groups showed a wide range of anticorrelation scores (younger adults:  $-0.43$  to  $0.35$ ; older adults:  $-0.53$  to  $0.53$  – see Fig. 2), however unlike previous studies (e.g., Spreng et al., 2016), there was no significant group difference in the average anticorrelation score,  $t < 1$ .

The first LV from the behavioral-PLS (the only significant LV,  $p < 0.05$ ) accounted for 41.99% of the covariance in the data and showed that increased activity in a common set of frontal, insular, and cingulate regions during the "ignore words" condition was associated with the extent of DAN-DMN anticorrelation and distractibility (Fig. 3a). These regions included common control areas such as bilateral inferior and left middle frontal gyri, left dorsal anterior insula (aINS), and anterior cingulate cortex (ACC) (see Table 2). These areas are considered to be part of control networks, such as the fronto-parietal and salience or cingulo-opercular networks (e.g., Dosenbach et al., 2008; Seeley et al., 2007; Vincent et al., 2008), and overlap with areas shown to modulate DMN activity (Chen et al., 2013; Wen et al., 2013). The PLS analysis also identified the bilateral superior temporal gyri, which among many functions, have been implicated in visual spatial orienting (e.g., Himmelbach et al., 2006), as well as a set of visual (e.g., inferior occipital gyrus and cuneus) and subcortical (e.g., putamen and thalamus) regions (Table 2). The latter subcortical structures (and other subcortical regions) have previously been shown to be part of the salience and fronto-parietal control networks (e.g., Seeley et al., 2007; Spreng et al., 2010) and are hypothesized to play a role in generally responding to salience (cognitive or emotional) and identifying that salience to higher order control regions (see Seeley et al., 2007).

As illustrated in Fig. 3b, the PLS analysis showed that activation in all the identified areas was associated with opposite patterns of DAN-DMN interaction and distractibility in the two age groups. Greater activation in these areas (as indicated by positive brain scores) was associated with increased DAN-DMN anticorrelation,  $r = -0.51$ , 95% CI [−0.35, −0.83], and less distractibility,  $r = -0.81$ , 95% CI [−0.76, −0.95], in older adults, but was associated with reduced DAN-DMN anticorrelation,  $r = 0.49$ , 95% CI [0.26, 0.83], and more distractibility,  $r = 0.58$ , 95% CI [0.45, 0.87], in younger adults. The brain-behavior relationships within each group were significantly different from one another (tested using Fisher's  $r$  to  $z$  transformation) for the association with DAN-DMN anticorrelation,  $z = 3.02$ ,  $p < 0.005$ , and distractibility,  $z = 4.92$ ,  $p < 0.0001$ , demonstrating that the expression of the outlined brain pattern was linked to opposite patterns of performance in the two age groups (i.e., better in older adults and worse in younger adults).

### Discussion

We tested the neural correlates of distraction control in younger and older adults in the context of DAN-DMN anticorrelation. These networks are known to have an intrinsic negative relationship, and the degree of their anticorrelation is associated with performance on tasks demanding externalized attention such as working memory and fluid intelligence tasks (e.g., Cole et al., 2012; Keller et al., 2015; Sala-Llonch et al., 2012). Here, we identified a set of brain regions, previously shown to be involved in DMN regulation (e.g., Chen et al., 2013; Wen et al., 2013), whose activity during a distraction control task correlated with the extent of the networks' anticorrelation and performance on the task. Although greater DAN-DMN anticorrelation was generally associated with better performance across both groups, engagement of control regions associated with the degree of anticorrelation predicted opposite patterns of network coupling and performance in each age group. In particular, recruitment of regions including bilateral inferior and left middle frontal gyri, left dorsal aINS, and ACC, was associated with greater DAN-DMN anticorrelation and better performance in older adults. This same neural pattern was associated with the opposite pattern of behavior in younger adults.



These age differences in associations were observed despite of a lack of group difference in the average DAN-DMN anticorrelation score, which has been reported in previous studies (e.g., Keller et al., 2015; Spreng et al., 2016). This lack of average group difference may possibly be related to the nature of the task used, as various task demands have been shown to influence the degree of the networks' anticorrelation (e.g., Leech et al., 2011). In particular, average group differences have typically been reported during rest or task conditions that require inwardly directed attention (such as autobiographical planning). In the current study, however, we used an externally-oriented distraction control task, which likely had different demands and posed a different level of challenge across all participants. Nevertheless, based on the high variability of the anticorrelation scores within each age group, our results suggest that younger adults who showed less DAN-DMN anticorrelation and experienced more interference from the distractors, engaged the outlined control areas in an unsuccessful attempt to ignore the distractors. In contrast, older adults who recruited the same areas showed greater DAN-DMN anticorrelation and were more successful at ignoring the distractors and performing the task, demonstrating a complex interaction between age, recruitment of control regions, network interaction, and cognitive performance.

The regions identified in the current study overlap with a set of regions involved in inhibiting distracting stimuli across a range of inhibitory control tasks (Laird et al., 2005; Nee et al., 2007b; Simmonds et al., 2008), and are consistent with previous studies examining “transmodal” or “hub” regions involved in coordinating brain network dynamics (e.g., Braga et al., 2013; van den Heuvel and Sporns, 2011, 2013). It follows that these regions may support cognitive control by enhancing network reconfiguration in response to changing task demands, ensuring an optimal functional organization for better task performance. For example, the left MFG has been shown to exhibit connectivity patterns with virtually all control and default mode regions, suggesting that it plays a role in coordinating interactions between large scale networks, which in turn, predicts behavioral performance on working memory and fluid intelligence tasks (Cole et al., 2012). Other regions such as the INS and ACC, which some consider to be part of a salience or cingulo-opercular network (Dosenbach et al., 2007, 2008; Seeley et al., 2007), have also been shown to support cognitive task performance by mediating the switching between externally and internally oriented brain networks and adjusting their activity in accordance with task demands (Goulden et al., 2014; Sridharan et al., 2008). In particular, these regions are hypothesized to sustain performance by supporting a multitude of cognitive operations. These operations include allocating attention to the processing of significant or salient stimuli (Uddin, 2015; Menon and Uddin, 2010), resolving ambiguity and conflict among competing response options (Botvinick et al., 2001; Botvinick et al., 1999; Milham et al., 2001), monitoring errors and aiding performance on demanding trials with longer reaction times (Dosenbach et al., 2006; Grinband et al., 2011), and using all performance feedback signals for the purpose of regulating task control and improving performance (Neta et al., 2014).

In the current study, we demonstrate that the extent of recruitment of those regions during a distraction control task is associated with opposite patterns of network interaction and behavioral performance in younger and older adults. Activity in such regions may have played a compensatory role in older adults by resolving the competition for computational resources that is thought to exist between the DAN and DMN (e.g., Anticevic et al., 2012a; Lustig et al., 2003; Persson et al., 2007), and allocating these resources more to the DAN for better distraction regulation. In younger adults, however, engagement of the same regions may imply greater interference from the DMN and external distractors, and an unsuccessful reliance on older-adult like neural mechanisms to resolve such interference. That is, relative to other younger adults who experienced less interference, those who relied on additional control regions (which aid older adults) to resist such interference, showed worse performance.

Consistent with the above interpretation, age-related differences in neural-behavioral association patterns have been observed in a large number of separate studies. For example, although over-recruitment of frontal and parietal regions has been associated with successful conflict resolution in various inhibitory control tasks in older adults (e.g., Langenecker et al., 2004; Vallesi et al., 2011; Zysset et al., 2007), greater activity in similar regions has been correlated with worse performance in younger adults (e.g., Minamoto et al., 2012; Nee et al., 2007a). Similarly, more recent studies have demonstrated that increased connectivity between control regions in younger adults is also associated with poorer cognitive control abilities. In particular, greater connectivity among DAN regions (Geerligs et al., 2014), strengthened causal interaction between the INS and ACC (Cai et al., 2015), and increased network communication (Spielberg et al., 2015) during the performance of control tasks, have all been associated with worse task performance in young adults. This suggests that younger adults, who generally experience greater cognitive demand (at particular task loads), are unsuccessfully relying on additional control mechanisms to meet those demands and show worse performance relative to others who rely less on such mechanisms. Evidence more consistent with the present findings comes from studies showing opposite brain-behavior correlations in younger and older adults for the same regions during task performance. In particular, Rypma and D'Esposito (2000) demonstrated that greater bilateral dlPFC activity during the retrieval phase of a delayed match-to-sample working memory task was associated with faster RTs in older adults but slower RTs in younger adults. Similarly, Motes et al. (2011) showed that greater bilateral MFG activity during a digit-symbol coding task of processing speed was associated with faster RT and higher accuracy in older adults but slower RT and lower accuracy in younger adults. Here, we extend those findings to network interaction patterns and demonstrate that activation of a common set of control regions is associated with age-related different DAN-DMN anticorrelation and performance patterns in distraction control tasks.

Although the DAN-DMN anticorrelation pattern was associated with better distraction control and is generally characteristic of better performance on externally oriented tasks, we stress that this largely occurs when behavior depends on external input. In alternate contexts, DMN activity has been linked to enhanced performance. In particular, activity in the DMN improves cognitive performance when the task relies on internally stored representations. For example, the DMN is associated with the organization of incoming information based on prior knowledge (Ames et al., 2015), recalling and reinstating memories and contexts (Chen et al., 2016), and better working memory for familiar stimuli (Spreng et al., 2014). In addition, DMN coupling with control regions has been associated with rapid memory recollection (Fornito et al., 2012), as well as internally focused goal-directed cognition, such as autobiographical planning (Spreng et al., 2010). Taken together, the evidence suggests that the link between large-scale network interaction patterns and behavior varies as a function of task and context. It remains an open question then, whether participants with reduced DAN-DMN anticorrelation and poorer distraction regulation would perform better than those with enhanced distraction control on internally-driven, DMN dependent tasks.

In conclusion, our findings demonstrate the complexity of the neural correlates of distraction control and illustrate how recruitment of control areas can be associated with opposite network interaction and behavioral performance patterns based on age. Although multiple studies have shown that the functional antagonism of the DAN and DMN is important for behavioral performance on externally oriented tasks, we demonstrate that the neural mechanisms associated with that network interaction pattern vary between individuals from different age groups. This provides further insight into the relationship between cognitive ability and large-scale network interactions and, in general, illustrates the intricacy of brain-behavior associations and how they can change with increasing age.

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