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# Heightened activity in a key region of the ventral attention network is linked to reduced activity in a key region of the dorsal attention network during unexpected shifts of covert visual spatial attention

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ABSTRACT

To enable unexpected shifts of covert visual spatial attention, a ventral attention network is thought to dampen activity in a dorsal attention network that maintains the current focus of attention. However, direct evidence to support this view is scarce. In the present study, we investigated this hypothesis by asking healthy young adults to perform a covert visual spatial attention task while their brain activity was recorded with functional magnetic resonance imaging (fMRI). In each trial, participants discriminated the orientation of a target-colored letter in the cued visual field (valid trials) or, occasionally, in the uncued visual field (invalid trials). Consistent with prior work, the ventral attention network was more active in invalid trials than in valid trials. Most importantly, functional connectivity analyses revealed that an increase of activity in the right inferior frontal gyrus (a key region of the ventral attention network) was linked to smaller increases of activity in (a) the right inferior parietal lobe (a key region of the dorsal attention network) and (b) the left dorsolateral prefrontal cortex and dorsal anterior cingulate cortex (other regions enabling the control of attention) in invalid trials, relative to valid trials. These findings provide novel support for the view that key regions of the ventral attention network help to enable unexpected shifts of covert visual spatial attention by dampening activity in brain regions that participate in maintaining the current focus of attention.



## Introduction

Current models posit that distinct brain networks enable different components of covert visual spatial attention (Corbetta and Shulman, 2002; Corbetta et al., 2008). A so-called "dorsal attention network", which classically includes the posterior parietal cortex (PPC) and the frontal eye fields (FEF), is thought to participate in orienting visual spatial attention (Corbetta et al., 2000; Giesbrecht et al., 2003; Hopfinger et al., 2000). More specifically, this network is thought to generate and maintain endogenous signals related to current task goals (Corbetta et al., 2000; Hopfinger et al., 2000), bias the activation of sensory (Weissman et al., 2004; Woldorff et al., 2004) and motor (Astafiev et al., 2003) regions of the brain that are important for achieving those goals, hold task-relevant information online in short-term memory (Pessoa et al., 2002), and link stimuli to responses (Rushworth et al., 2001) (for a review, see Corbetta et al., 2008). The dorsolateral prefrontal cortex (DLPFC) and portions of the dorsal anterior cingulate cortex (dACC) have been implicated in related control processes (Dosenbach et al., 2006; Orr and Weissman, 2009; Posner and DiGirolamo, 1998; Weissman et al., 2004; Woldorff et al., 2004). In contrast, a so-called "ventral attention network", which classically includes the right inferior frontal gyrus (IFG) and the right temporal–parietal junction (TPJ), is thought to make important contributions to stimulus-driven *reorienting* of covert visual spatial attention (Corbetta et al., 2000; Serences et al., 2005). When a relevant stimulus appears at an unexpected location, this network is thought to generate an "interrupt signal" that helps to terminate the current focus of attention, thereby enabling spatial attention to move to a new location (Corbetta et al., 2008).

Interactions between the dorsal and ventral attention networks are also thought to make important contributions to reorienting covert visual spatial attention (Corbetta et al., 2008). In particular, the "interrupt signal" generated by the ventral attention network is thought to facilitate the process of reorienting covert visual spatial attention by dampening activity in regions of the dorsal attention network that maintain the current focus of attention. The ventral attention network may not initiate the reorienting response:

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electrophysiological studies suggest that the latency of neural responses to visual stimuli is not typically shorter in the ventral than in the dorsal attention network (see Corbetta et al., 2008 for a review). Instead, the dorsal attention network may initiate the process of reorienting spatial attention while late-arriving signals from the ventral attention network are necessary to complete this process (Corbetta et al., 2008).

Several findings indirectly support the hypothesis that interactions between the dorsal and ventral networks contribute to reorienting covert visual spatial attention. First, lesions to the ventral attention network are linked to disrupted activity and functional connectivity in the PPC (a key region of the dorsal attention network), and the magnitude of these disruptions predicts the degree to which neglect patients are impaired at reorienting spatial attention to targets in the contralesional visual field (He et al., 2007). Second, damage to the superior longitudinal fasciculus, which connects inferior parietal regions in the TPJ to dorsal frontal regions that contribute to orienting spatial attention (e.g., the FEF and the DLPFC), is associated with the rightward spatial bias that typically characterizes neglect (Shinoura et al., 2009; Thiebaut de Schotten et al., 2005). Third, the dorsal and ventral attention networks are coactivated in functional neuroimaging studies of healthy controls during unanticipated shifts of covert visual spatial attention (Corbetta et al., 2002; Kincade et al., 2005).

However, these sorts of findings provide only weak evidence that interactions between the dorsal and ventral attention networks contribute to reorienting covert visual spatial attention. First, lesion studies reveal which brain regions are *necessary* to perform a task, but do not reveal whether these regions underlie critical task operations in isolation or by interacting with other regions (Weissman and Banich, 1999). Second, and similarly, functional neuroimaging studies of healthy controls showing coactivation of the dorsal and ventral attention networks during unanticipated shifts of covert visual spatial attention do not reveal whether these networks are working in isolation or interacting with each other (Wen et al., 2012). Thus, the available evidence does not conclusively show that interactions between the dorsal and ventral attention networks contribute to reorienting covert visual spatial attention.

Stronger evidence to support this view could be provided by functional neuroimaging studies linking unanticipated shifts of covert visual spatial attention to changes of functional connectivity between key regions of the dorsal and ventral attention networks. Along these lines, a recent fMRI study assessed functional connectivity between the dorsal and ventral networks during a covert visual spatial attention task (Wen et al., 2012). However, this study focused on how functional connectivity between these networks varied with measures of behavioral performance, rather than on how it varied with the requirement to reorient covert visual spatial attention. Thus, although interactions between the dorsal and ventral attention networks are thought to make crucial contributions to reorienting covert visual spatial attention in the healthy brain, little evidence directly supports this hypothesis.

In the present study, we tested this hypothesis by reanalyzing data from one of our previously published fMRI studies of covert visual spatial attention (Prado and Weissman, 2011). Specifically, we determined whether one or more key regions of the ventral attention network play a role in dampening activity in key regions of the dorsal attention network during unexpected shifts of covert visual spatial attention. In our study, a group of healthy adults performed a covert spatial attention task while we recorded their brain activity using fMRI (Fig. 1). At the beginning of each block, participants were cued to attend to stimuli appearing in the left visual field (LVF) or to stimuli appearing in the right visual field (RVF). Subsequently, in each of several trials, they discriminated the orientation of a target-colored letter, which was usually presented in the cued visual field (valid trials) but occasionally appeared in the uncued visual field (invalid trials), while ignoring a simultaneous non-target-colored distractor letter in the opposite visual field.

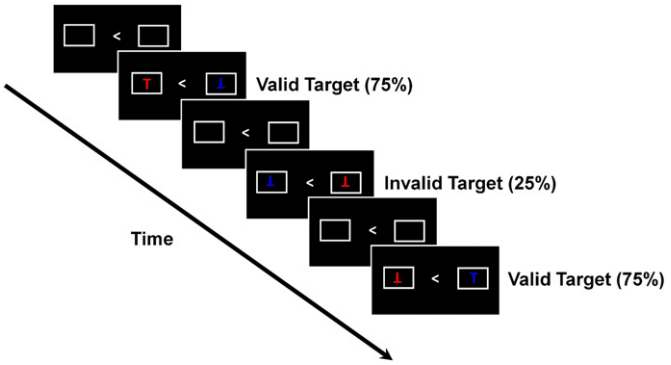


**Fig. 1.** The covert visual spatial attention task. At the start of each 68 s block, a cue (< or >) instructed participants to covertly attend to stimuli in either the left or the right visual field. Next, in each of 12 subsequent trials (trial duration, 3750 ms), participants discriminated the orientation (i.e., upright or inverted) of the "T" that appeared in a pre-specified, relevant color (e.g., red; duration, 100 ms) while ignoring a simultaneous "T" in the opposite visual field that appeared in a different, irrelevant color (e.g., blue; duration, 100 ms). In valid trials (75%), the "T" in the pre-specified color (e.g., red) appeared in the cued visual field. In invalid trials (25%), it appeared in the uncued visual field. Variable periods of visual fixation (ranging from 0 ms to 3750 ms, in units of 1250 ms) were inserted between (a) the cue and the first trial in each block and (b) all 12 trials within each block. Trials were presented in a pseudo-random order, such that at least one valid trial preceded and followed each invalid trial.

We made two predictions. First, consistent with prior findings (Corbetta et al., 2000), we predicted greater activity in ventral attention network regions in invalid trials, relative to valid trials. Second, we predicted that an increase of activity in the right IFG and/or the right TPJ within the ventral attention network would be linked to smaller increases of activity in key regions of the dorsal attention network in invalid trials, relative to valid trials. The latter effect would provide novel support for the hypothesis that key regions of the ventral attention network dampen activity in key regions of the dorsal attention network during unanticipated shifts of covert visual spatial attention.

## Materials and methods

### *Participants*

Seventeen right-handed volunteers with no history of neurological or psychiatric disorders participated in the study. All had normal hearing and normal or corrected-to-normal vision. Participants gave written informed consent before the experiment began and were paid for their participation when the experiment ended ($20 per hour). The experimental procedures were approved by the University of Michigan Biomedical and Health Sciences Institutional Review Board. Data from 3 participants were excluded from the main analyses because of excessive head movement (i.e., greater than 3 mm; n = 2) and unusable eye-tracker recordings (n = 1). The 14 remaining participants (5 males) were aged between 18 and 22 years (mean age = 20 years).

### *Stimuli and task parameters*

A detailed description of the covert visual spatial attention task (Fig. 1) was provided in Prado and Weissman (2011). Briefly, each run of the experiment was divided into 6 blocks (68 s each). At the start of each block, a cue (< or >; size, 1.70° × 1.55°) instructed participants to attend to stimuli appearing in the LVF or to stimuli

appearing in the RVF. The cue remained on the screen throughout the entire 68 s block.

Each block contained 12 trials (3.75 s) in which two letter "Ts" (one blue and one red; size, 2.9°×2.1°) were presented simultaneously for 100 ms. One T appeared 8° to the left of fixation and the other appeared 8° to the right of fixation. Participants were instructed to discriminate the orientation of the T that appeared in a prespecified, relevant color (blue or red; half of the participants were instructed to discriminate blue Ts throughout the study while the other half were instructed to discriminate red Ts). The orientation of the Ts (i.e., right side up or upside down) was varied independently in the two visual fields across trials. In most trials (i.e., valid trials), the T in the relevant color appeared in the cued visual field (e.g., the RVF). In some trials (i.e., invalid trials), however, the T in the relevant color appeared in the opposite visual field (e.g., the LVF). Each block contained nine valid trials (75%) and three invalid trials (25%). Finally, the trials were presented using a pseudo-random order in which each invalid trial was preceded and followed by at least one valid trial.

The intertrial interval (ITI) within each block ranged from 0 to 3 TRs (in units of 1.5 s TR) and followed a roughly exponential distribution that favored short ITIs (Ollinger et al., 2001a, 2001b). The same jittering method was applied to the interval between the onset of the cue at the beginning of each block and the first trial of the block. Finally, the first block of each run was preceded by 15 s of visual fixation and the last block was followed by 30 s of visual fixation.

Visual stimuli were generated using Presentation software (Neurobehavioral Systems, www.neurobs.com). In each trial, participants indicated the orientation of the T in the relevant color by pressing either a left key or a right key on an MR-compatible keypad using the index finger or the middle finger of their right hand.

### *Eye tracking data analysis*

An infrared video eye-tracker (NordicNeuroLab, Bergen, Norway) was used to record eye position and pupil size in the scanner (recording frequency = 60 Hz). The eye tracker was calibrated before each run at fixation (central position) and 8 eccentric points. Eye position traces from −100 to +400 ms post-stimulus onset were analyzed off-line. Saccade velocity (i.e., the derivative of the horizontal eye-position trace) was used to identify trials in which fixation was broken. Pupil size was used to identify trials in which participants blinked. A trial was excluded from fMRI analyses when (1) saccade velocity exceeded 30°/s or (2) pupil size was equal to zero (Macaluso et al., 2002). Two participants had one run in which more than 30% of the trials were rejected after eye-tracker analysis. These two runs were excluded from further fMRI analyses.

### *Imaging procedures*

Images were acquired with a 3-T GE Signa scanner (General Electric, Milwaukee, WI) equipped with a standard quadrature head coil. The fMRI blood oxygenation level dependent (BOLD) signal was measured with a reverse spiral imaging sequence (repetition time [TR] = 1250 ms, echo time [TE] = 30 ms). Twenty-seven contiguous axial slices were acquired in each functional image (4.50-mm thick, field of view, 22 cm; in-plane resolution, 3.44×3.44 mm). A total of 351 functional images were acquired in each run. No trials were presented during the first six of these images, and these images were discarded to allow for T1 equilibration effects.

Following functional image acquisition, we acquired a 3D spoiled gradient echo (SPGR), high-resolution, T1-weighted anatomical image for each participant (TR = 10.5 ms, TE = 3.4 ms, FOV = 24 mm, flip angle = 25°, slice thickness = 1.5 mm).

### *fMRI preprocessing*

There were several preprocessing steps. First, fluctuations of the BOLD signal in each run that correlated with a participant's respiration and heartbeat (measured during the experiment) were removed from the data (Hu et al., 1995). Second, using Statistical Parametric Mapping (SPM5, http://www.fil.ion.ucl.ac.uk/spm), the functional images were corrected for slice acquisition delays and spatially realigned to the first volume of the first run to correct for head movements. For each of two participants, one run of functional images was not further analyzed due to head movements greater than 3 mm. Finally, the functional images were normalized to the standard Montreal Neurological Institute (MNI) template volume (normalized voxel size, 3.75×3.75×4.5 mm) and smoothed with an 8 mm isotropic Gaussian kernel.

### *fMRI processing*

In each participant, we conducted event-related regression analyses of the fMRI data using the general linear model. In our particular model, a standard hemodynamic response function was used to model the fMRI signal in each trial (Josephs et al., 1997). However, we excluded from all analyses incorrect trials (2.5% of trials) and correct trials in which RT was greater than three standard deviations from the mean of the corresponding trial type (1.5% of trials). There were six regressors of interest in each run: (1) attend LVF cue, (2) attend RVF cue, (3) valid LVF target, (4) valid RVF target, (5) invalid LVF target, and (6) invalid RVF target. We also included nuisance regressors in each run to model (1) trials that were excluded from the analyses and (2) motion parameters. Finally, a high pass filter with a cutoff period of 128 s was applied and serial correlations were corrected using an autoregressive AR(1) model. Group results were obtained by performing random effects analyses on participant-specific beta values using SPM5.

### *Psychophysiological interaction (PPI) analyses*

We used two whole-brain PPI analyses to assess condition-specific changes in functional connectivity (Friston et al., 1997; Gitelman et al., 2003). Each PPI analysis determined whether an increase of activity in a key region of the ventral attention network – the right IFG or the right TPJ – was linked to a smaller increase of activity elsewhere in the brain in invalid trials, relative to valid trials. The coordinates for each of these two seed regions – the right IFG and the right TPJ – were determined using a whole-brain random effects analysis, which identified brain regions showing greater activity in invalid than in valid trials. In each participant, we created two volumes of interest (spheres, 6 mm radius) centered on these coordinates. These volumes of interest served as the seed regions in our PPI analyses.

As described above, two PPI analyses were conducted for each participant: one in which the right IFG served as the seed region and a second in which the right TPJ served as the seed region. Three regressors were included in each PPI analysis: (1) the time course of activity in the seed region as defined by the first eigenvariate (i.e., the "physiological" regressor), (2) the contrast of invalid versus valid trials after convolution with a synthetic HRF (i.e., the "psychological" regressor), and (3) the interaction between the first two regressors (i.e., the "psychophysiological interaction" regressor). The psychological interaction regressor was constructed in two steps (Gitelman et al., 2003): (1) multiplying the deconvolved time series of the seed region by the psychological contrast regressor and (2) convolving the resulting interaction term with a synthetic HRF. Group results were obtained by performing random effects analyses on participant-specific beta values using SPM5.

*Voxelwise analyses*

Significant activation clusters were identified using a height threshold of $p<0.01$ and a cluster extent threshold of 45 contiguous voxels. These thresholds were determined by a Monte Carlo simulation (5000 iterations) conducted using the 'AlphaSim' program (http://afni.nimh.nih.gov/pub/dist/doc/manual/AlphaSim.pdf). Of importance, they enabled family-wise error (FWE) correction for multiple comparisons at $p<0.05$ for the entire brain volume. Activations that were common to multiple voxelwise maps were determined using a conjunction analysis, in which we created Boolean intersections of individual activation maps. All coordinates are reported in MNI space.

*Region of interest analyses*

We used an SPM toolbox called "Marsbar" (http://marsbar.sourceforge.net/) to conduct region of interest (ROI) analyses. Each ROI contained all voxels within a 6 mm radius of a coordinate of interest. In each participant, the fMRI signal for each trial type was averaged across all voxels in a ROI. Unless otherwise noted, we report two-tailed $p$ values.

## Results

*Task performance*

The behavioral results were previously reported in the original analysis of these data (Prado and Weissman, 2011), but are summarized again for completeness.

We performed two within-participant ANOVAs (one on mean RT and one on mean error rate) with validity (valid, invalid) and direction of spatial attention (left, right) as factors. Although the analysis of mean error rates did not reveal any main effects or interactions (the overall mean error rate was quite low at 2.47%), the analysis of mean RT revealed both a main effect of validity and an interaction between validity and direction of spatial attention. First, in line with prior work (Posner, 1980), the main effect of validity indicated that mean RT was significantly longer in invalid trials (631 ms) than in valid trials (594 ms), $F(1,13)=29.69$, $p<0.0015$. Second, and unexpectedly, the increase in RT observed in invalid compared to valid trials was larger when attention was directed to the left visual field (639 ms vs. 585 ms) as compared to the right visual field (623 ms vs. 604 ms), $F(1,13)=5.99$, $p<0.029$. As predicted, however, the main effect of validity was significant in both visual fields (LVF: $t(13)=6.06$, $p<0.001$; RVF: $t(13)=1.89$, $p=0.0407$; we used one-tailed t-tests here because there was an *a priori* hypothesis that mean RT should be longer in invalid trials than in valid trials).

*Eye movements*

As detailed in the Materials and methods section, trials were not included in the fMRI analyses if they were contaminated by eye movements between 100 ms before and 400 ms after stimulus onset. Further, to verify that eye movements (i.e., eye position and eye velocity) were not different in the valid LVF target and valid RVF target trials that we *did* include in the fMRI analyses, we used a larger temporal window around stimulus onset (−3000 to +3000 ms). Specifically, we divided the eye movement data into 12 successive time bins of 500 ms each and used separate within-participant ANOVAs to analyze (a) the average eye position data and (b) the average eye velocity data in each bin. There were two factors in each ANOVA: direction of attention (left, right) and time (0–500 ms). As we reported in a prior analysis of these data (Prado and Weissman, 2011), none of the resulting 24 ANOVAs revealed either (a) a significant main effect of direction of attention (all $p>0.05$) or (b) a significant interaction between direction of attention and time (all $p>0.05$). Thus, there was no evidence to suggest that participants' eye movements differed in valid LVF target and valid RVF target trials.

*fMRI*

*Validity modulates activity in the right IFG and the right TPJ*

In order to test our hypothesis about functional connectivity between the dorsal and ventral attention networks during unexpected shifts of covert visual spatial attention, it was first necessary to identify regions in the ventral attention network that showed a validity effect. Consistent with prior findings (Corbetta et al., 2000, 2008), a voxelwise analysis revealed greater activity in the right IFG ($x=45$, $y=10$, $z=0$) and the right TPJ (middle temporal gyrus: $x=48$, $y=-65$, $z=14$) in invalid trials, relative to valid trials (Fig. 2; Table 1). Using these activations, we created two seed regions for the functional connectivity analyses that allowed us to test our hypothesis (see Materials and methods).

*Validity modulates functional connectivity between the right IFG and key regions of the dorsal attention network*

We hypothesized that an increase of activity in the right IFG and/or the right TPJ of the ventral attention network would be linked to a smaller increase of activity in key regions of the dorsal attention network in invalid trials, relative to valid trials. To test this hypothesis for the right IFG, we performed a conjunction analysis to determine which brain regions showed both (a) less functional connectivity with the right IFG in invalid than in valid trials and (b) increased activity for attend LVF and attend RVF cues, relative to activity during fixation (i.e., orienting-related activity). As hypothesized, the conjunction analysis identified a key region of the dorsal attention network — the right PPC (Precuneus: $x=21$, $y=-76$, $z=36$; right inferior parietal lobe: $x=58$, $y=-31$, $z=36$). Also consistent with predictions, the conjunction analysis identified related control regions in the left DLPFC (Middle Frontal Gyrus: $x=-31$, $y=34$, $z=32$) and the dACC (Cingulate Gyrus: $x=7$, $y=10$, $z=45$) (Fig. 3; Table 2). ROI analyses did not reveal additional activation differences between attend left and attend right cues in these regions, likely because these cues imposed similar overall demands on control processes that orient spatial attention. Nonetheless, the results of the conjunction analysis support our hypothesis that, during unexpected shifts of covert visual spatial attention, the right IFG dampens activity in key regions of the dorsal attention network and related control regions.

*Validity does not modulate functional connectivity between the right TPJ and key regions of the dorsal attention network*

We next investigated whether a change of activity in the right TPJ was linked to a smaller change of activity in key regions of the dorsal attention network in invalid trials, relative to valid trials. A voxelwise PPI analysis involving the right TPJ seed region revealed no such effects anywhere in the brain.

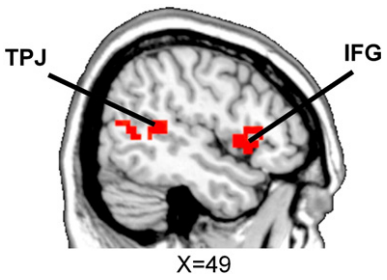


**Fig. 2.** Brain regions showing greater activity in invalid trials than in valid trials. These regions included the right inferior frontal gyrus (right IFG) and the right temporo-parietal junction (right TPJ). All activations are overlaid on slices of the MNI-normalized anatomical brain.

**Table 1**
Brain regions showing greater activity in invalid than in valid trials.

| Anatomical location | ~ BA | MNI coordinates | | | Z-score |
|---|---|---|---|---|---|
| | | *X* | *Y* | *Z* | |
| L. precuneus | 7 | −7 | −52 | 50 | 3.83 |
| L. superior parietal lobule | 7 | −7 | −69 | 58 | 3.75 |
| L. subcallosal gyrus | 25 | −10 | 24 | −14 | 3.57 |
| L. inferior frontal gyrus | 47 | −38 | 17 | −4 | 3.04 |
| R. inferior frontal gyrus | 47 | 45 | 10 | 0 | 3.17 |
| L. medial frontal gyrus | 9 | −14 | 41 | 27 | 3.18 |
| R. anterior cingulate | 24 | 10 | 28 | 18 | 3.08 |
| R. middle temporal gyrus | 19 | 48 | −65 | 14 | 3.1 |
| R. middle temporal gyrus | 39 | 55 | −55 | 4 | 3.01 |

Notes. L., left; R. right; ~BA, approximate Brodmann Area; MNI, Montreal Neurological Institute.

**Table 2**
Brain regions showing both (a) less functional connectivity with the right IFG in invalid than in valid trials and (b) greater activity for attend LVF and attend RVF cues relative to baseline (i.e., orienting-related activity).

| Anatomical location | ~ BA | MNI coordinates | | |
|---|---|---|---|---|
| | | X | Y | Z |
| R. middle temporal gyrus | 37 | 58 | −58 | −14 |
| R. precuneus | 7 | 21 | −76 | 36 |
| R. angular gyrus | 39 | 31 | −69 | 32 |
| L. middle frontal gyrus | 9 | −31 | 34 | 32 |
| R. lingual gyrus | 18 | 14 | −82 | −14 |
| R. postcentral gyrus | 40 | 65 | −28 | 22 |
| R. inferior parietal lobule | 40 | 58 | −31 | 36 |
| R. postcentral gyrus | 40 | 55 | −31 | 22 |
| R. cingulate gyrus | 32 | 7 | 10 | 45 |
| L. middle occipital gyrus | 18 | −14 | −100 | 9 |
| L. middle occipital gyrus | 19 | −31 | −93 | 14 |
| L. cuneus | 19 | −14 | −93 | 32 |
| R. supramarginal gyrus | 40 | 41 | −41 | 36 |

Notes. L., left; R. right; ~BA, approximate Brodmann Area; MNI, Montreal Neurological Institute.

## Discussion

Although interactions between key regions of the dorsal and ventral attention networks are thought to make important contributions to covert visual spatial attention, direct evidence supporting this view is scarce. In the present study, we therefore investigated the hypothesis that key regions of the ventral attention network dampen activity in key regions of the dorsal attention network during unexpected shifts of covert visual spatial attention. Our findings provide novel support for this hypothesis.

### *Heightened activity in a key region of the ventral attention network is linked to reduced activity in a key region of the dorsal attention network during unexpected shifts of covert visual spatial attention*

A ventral attention network is thought to enable reorienting covert visual spatial attention by dampening activity in a dorsal attention network that maintains the current focus of attention (Corbetta et al., 2008). Consistent with this hypothesis, the present study revealed a change of functional connectivity between key regions of the ventral and dorsal networks during unexpected shifts of covert visual spatial attention. Specifically, an increase of activity in the right IFG (a key region of the ventral attention network) was linked to smaller increases of activity in the right PPC (a key region of the dorsal attention network) and in the dACC and left DLPFC (other regions that underlie the control of attention) when participants were required to reorient visual spatial attention (invalid trials), relative to when they were not (valid trials). These findings are consistent with other recent data linking recruitment of the right IFG to unexpected shifts of covert visual spatial attention (Shulman et al., 2009). Most importantly, they provide novel support for the view that interactions between key regions of the ventral and dorsal attention networks make important contributions to reorienting visual spatial attention.

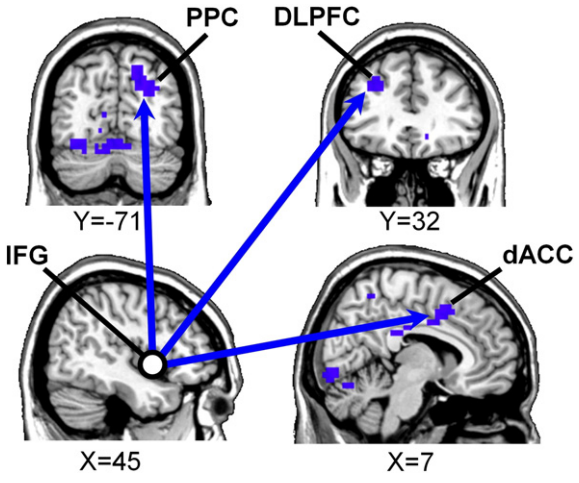


**Fig. 3.** Conjunction analysis. These brain regions show less functional connectivity with the right IFG seed region (white circle) in invalid trials than in valid trials *and* greater activation for "Attend LVF" and "Attend RVF" cues versus baseline. These regions include the right PPC, the left DLPFC, and the dACC. All activations are overlaid on slices of the MNI-normalized anatomical brain.

One might wonder whether the functional connectivity effects above were driven by bottom-up processes that reorient spatial attention to salient stimuli, rather than by top-down processes that reorient spatial attention to relevant stimuli. However, there are several reasons why bottom-up processes likely do not account for these effects. First, valid and invalid trials were matched in terms of bottom-up salience: they each contained two differently-colored letters. Second, the ventral attention network is not recruited during purely bottom-up shifts of spatial attention to salient irrelevant stimuli (Kincade et al., 2005), unless such stimuli possess task-relevant sensory features (Natale et al., 2010; Serences et al., 2005) or are novel and particularly surprising (Asplund et al., 2010). Third, damage to the ventral attention network enhances the ability of irrelevant stimuli to capture spatial attention (Ptak and Schnider, 2010), thereby indicating that bottom-up processes are stronger when the ventral attention network is damaged than when it is intact. These prior findings suggest that the present functional connectivity effects involving the ventral attention network were probably not driven by bottom-up processes.

We did not observe similar changes of functional connectivity between the right TPJ and key regions of the dorsal attention network. However, the literature suggests that such interactions may be less likely to occur when the probability of shifting covert visual spatial attention is relatively low, as in the present study, than when it is relatively high. When the probability of an invalid target is relatively low, the right TPJ is deactivated prior to target presentation, which may serve to inhibit shifts of attention to unimportant objects (Shulman et al., 2003). In contrast, when the probability of an invalid target is relatively high, a cue to attend a particular spatial location produces less deactivation in the right TPJ, which may serve to facilitate shifts of spatial attention to upcoming invalid targets (Doricchi et al., 2010) via interactions between the right TPJ and key regions of the dorsal attention network (Corbetta et al., 2008). Consistent with the latter possibility, increased interactions between the right TPJ and key regions of the dorsal attention network are observed when a contextual cue signals a relatively high probability that a simultaneous target is present at a different location (Geng and Mangun, 2011).

Given these findings, future work should investigate whether the probability of shifting covert visual spatial attention (high versus low) influences interactions between the right TPJ and key regions of the dorsal attention network during both (a) cue-triggered orienting of spatial attention and (b) target-triggered reorienting of spatial attention.

Future work might also investigate whether key regions of the dorsal attention network suppress activity in key regions of the ventral attention network to *prevent* shifts of covert visual spatial attention (Corbetta et al., 2008). For example, such suppression is thought to explain reduced activity in key regions of the ventral attention network when optimal task performance requires strongly focusing attention at a single location (Shulman et al., 2003). If this hypothesis is correct, then an increase of activity in key regions of the task-positive network should be linked to smaller increases of activity in key regions of the ventral attention network when a task requires strongly (versus weakly) focused attention at a particular location. Combined with the present findings, such a result would support the view that whether spatial attention needs to be maintained or shifted, respectively, influences whether dorsal attention network regions suppress activity in ventral attention network regions or vice-versa (Corbetta et al., 2008).

### *Relevance of the present findings to other conceptualizations of the ventral attention network*

It has been suggested that the "interrupt signal" generated by the ventral attention network also facilitates changes of attentional set outside the realm of spatial attention (Corbetta et al., 2008). These changes include transitions between rest and active task performance (Dosenbach et al., 2006; Fox et al., 2005), shifts of attention between internal thoughts supported by a so-called "default-mode network" (Christoff et al., 2009; Mason et al., 2007; Raichle et al., 2001; Weissman et al., 2006) and external stimuli in the environment (Corbetta et al., 2008), and shifts of attention that accompany a violation of social expectations (Mitchell, 2008; Pelphrey et al., 2004). Given the present findings, future studies might investigate whether key regions of the ventral attention network facilitate such transitions by dampening activity in brain networks that support newly-irrelevant attentional states.

Another conceptualization of the ventral attention network posits a crucial role for the right IFG in response inhibition (Aron et al., 2003). The present findings are not inconsistent with this view as shifting covert visual spatial attention may involve programming an eye movement to a new location while inhibiting the execution of an actual saccade (Moore et al., 2003; Rizzolatti et al., 1987). Moreover, response inhibition has been linked to regions of the right IFG, right PPC, and dACC/pre-supplementary motor area that are similar to those whose functional connectivity was probed in the present study (Aron and Poldrack, 2006; Sharp et al., 2010).

If the region of right IFG that we have identified plays a specific role in response inhibition (rather than a general role in terminating newly-irrelevant attentional states as discussed above), then additional studies will be needed to determine whether this contribution is direct or indirect. The right IFG may make a direct contribution via its connections with subcortical motor areas such as the subthalamic nucleus (Aron et al., 2007). Or, it may make an indirect contribution by signaling the presence of infrequent relevant stimuli to the dorsal attention network and other control regions (Doricchi et al., 2010; Shulman et al., 2009) which, in turn, inhibit responses that are no longer relevant (Sharp et al., 2010). Finally, distinct regions of the right IFG may underlie each of these contributions (Verbruggen et al., 2010). For these reasons, additional studies will be needed to further characterize the functional connectivity effects that we have observed.

### *Limitations*

An important limitation of the present study is that PPI analyses do not provide complete information about communication between a seed region and a target region (Friston et al., 1997). First, they do not allow firm inferences about the direction of communication between these regions (i.e., about which region sends a signal and which region receives a signal). Second, they do not exclude the possibility that activity in a seed region correlates with activity in a target region simply because these regions receive similar inputs from a third region. Given these caveats, future studies should seek converging evidence that unexpected shifts of covert visual spatial attention are linked to heightened interactions between the right IFG and key regions of the dorsal attention network.

Another limitation concerns our view that the dampened activity we observed in the right PPC, dACC, and left DLPFC reflected an inhibition of processes that maintain the current focus of spatial attention. Consistent with this possibility, each of these three regions was activated by attention-directing cues, which are thought to recruit processes that create and maintain a focus of attention (Corbetta et al., 2000; Hopfinger et al., 2000; Weissman et al., 2004). However, such cues likely also recruit other processes that are enabled by the dorsal attention network and related control regions, such as those that interpret the meaning of cue stimuli (Woldorff et al., 2004) and those that prepare upcoming responses (Astafiev et al., 2003). Thus, the effects we observed may have reflected the inhibition of processes other than those that maintain the current focus of attention. For this reason, future studies will be needed to further investigate the specific nature of the effects we observed.

## Conclusion

The present findings provide novel support for the hypothesis that the ventral attention network dampens activity in the dorsal attention network during unanticipated shifts of spatial attention (Corbetta et al., 2008). Specifically, they provide the first direct evidence from healthy controls that heightened activity in a key region of the ventral attention network (the right IFG) is linked to reduced activity in a key region of the dorsal attention network during unanticipated shifts of covert visual spatial attention. Future studies aimed at further characterizing the effects we have observed will continue to advance our understanding of how interactions between key regions of the dorsal and ventral networks contribute to attention.

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