



## Ventral fronto-parietal contributions to the disruption of visual working memory storage



Jonathan G. Hakun<sup>a,\*</sup>, Susan M. Ravizza<sup>b</sup>

<sup>a</sup> Department of Psychology, The Pennsylvania State University, University Park, PA, USA

<sup>b</sup> Department of Psychology, Michigan State University, East Lansing, MI 48824, USA

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### ABSTRACT

The ability to maintain information in visual working memory (VWM) in the presence of ongoing visual input allows for flexible goal-directed behavior. Previous evidence suggests that categorical overlap between visual distractors and the contents of VWM is associated with both the degree to which distractors disrupt VWM performance and activation among fronto-parietal regions of cortex. While within-category distractors have been shown to elicit a greater response in ventral fronto-parietal regions, to date, no study has linked distractor-evoked response of these regions to VWM performance costs. Here we examined the contributions of ventral fronto-parietal cortex to the disruption of VWM storage by manipulating memoranda-distractor similarity. Our results revealed that the degree of activation across cortex was graded in a manner suggesting that similarity between the contents of VWM and visual distractors influenced distractor processing. While abrupt visual onsets failed to engage ventral fronto-parietal regions during VWM maintenance, objects sharing categorical- (Related objects) and feature-overlap (Matched objects) with VWM elicited a significant response in the right TPJ and right AI. Of central relevance, the magnitude of activation in the right AI elicited by both types of distractor objects subsequently predicted costs to binding change detection accuracy. In addition, Related and Matched distractors differentially affected ventral-dorsal connectivity between the right AI and dorsal parietal regions, uniquely contributing to disruption of VWM storage. Together, our current results implicate activation of ventral fronto-parietal cortex in disruption of VWM storage, and disconnection between ventral frontal and dorsal parietal cortices as a mechanism to protect the contents of VWM.

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### Introduction

The ability to maintain information in working memory is a critical feature of the cognitive system that allows for goal-directed behavior. Short-term visual representation in the form of visual working memory (VWM) supports key functions such as selective attention to the visual environment and the ability to integrate visual information over time (Chun et al., 2011; Gazzaley and Nobre, 2012; Hollingworth et al., 2008; Postle, 2006; Woodman et al., 2013). The success of these functions, however, largely depends on the ability to avoid loss of internally represented information in VWM when encountering new, potentially distracting, visual information. While the neural mechanisms that support robust maintenance in VWM as well as suppression of irrelevant visual information have been investigated (Anticevic et al., 2010a,b; Clapp et al., 2010; Dolcos et al., 2007; Gazzaley and Nobre, 2012; Jha et al., 2004; Yoon et al., 2006), the neural pathways involved in disruption of storage in VWM remain poorly understood. In the current study, we investigated the contribution of the ventral fronto-parietal network

to the disruption of storage in VWM through a visual distraction paradigm.

Visual selective attention and VWM are often described as highly overlapping cognitive constructs (Chun, 2011; Cowan, 1999). Yet, to date, distraction effects within attention and working memory domains have been studied largely independently of one another. Results from studies of distraction during selective attention tasks (e.g. visual search) have coalesced into a prominent two-network theory of attentional control, often referred to as the “orienting” networks model (Corbetta et al., 2008; Yantis, 2008; Petersen and Posner, 2012; Power and Petersen, 2013) which suggests that top-down and bottom-up constituents of attentional control are situated dorsally and ventrally in the cortex, respectively. According to the two-network model, dorsal fronto-parietal cortex is responsible for maintaining plans for where and how to allocate attention to visual features or locations in space. Ventrally situated fronto-parietal regions, on the other hand, are thought to contribute a reorienting signal to dorsal regions in the presence of behaviorally relevant information in the environment. Supporting this interpretation, activation of the ventral network has been observed during attention capture to distracting visual information that is similar to the target of visual search (i.e. contingently salient information), whereas salient visual events lacking a relation to the

\* Corresponding author at: Department of Psychology, The Pennsylvania State University, University Park, PA 16802-3104, USA. Tel.: +1 814 867 2441.

E-mail address: [jgh5196@psu.edu](mailto:jgh5196@psu.edu) (J.G. Hakun).

search target (e.g. abrupt visual onsets/feature singletons) often only engage the dorsal network (Folk et al., 1992; de Fockert et al., 2004; Kincade et al., 2005; Serences et al., 2005).

Neuroimaging studies manipulating the similarity between memoranda and distractors suggest that behavioral relevance, likewise, may play a role in the disruption of VWM storage. Categorically overlapping distractors are more disruptive of VWM performance and result in increased functional recruitment throughout dorsal and ventral fronto-parietal cortices compared to task-irrelevant distractors (e.g. face distractors during VWM for faces, Dolcos et al., 2007; Gazzaley and Nobre, 2012; Jha et al., 2004; Yoon et al., 2006). This suggests that within-category distractors are perceived as behaviorally relevant and potentially receive greater processing (Clapp et al., 2010). However, it remains unclear whether the behavioral relevance of distractors would influence activation within both networks or remain more selective to the ventral network. For example, based on previous evidence using visual search (Dolcos et al., 2007; Gazzaley and Nobre, 2012; Jha et al., 2004; Yoon et al., 2006), we might expect to observe greater overall activation magnitudes with increasing memoranda–distractor similarity in the dorsal network regardless of behavioral relevance, whereas activation in the ventral network may be selective to behaviorally relevant distractors (Serences et al., 2005).

According to the two-network model, the ventral network is comprised of several nodes distributed across ventral fronto-parietal cortex including the right anterior insula (AI) and right temporo-parietal junction (TPJ). Recent studies have shown that the ventral fronto-parietal network tends to be suppressed during goal-directed behavior and particularly during VWM encoding (Anticevic et al., 2010b; Todd et al., 2005). While suppression of the ventral network has been linked with a lack of awareness of transient visual onsets (Todd et al., 2005) and successful encoding of information into VWM (Anticevic et al., 2010b), further work found that regions such as the right TPJ and AI are activated by the presence of salient visual distractors (Anticevic et al., 2010a; Anticevic et al., 2010b). This increase in ventral network activation during visual distraction could indicate that disruption of VWM storage involves a behavioral relevance mechanism; however, no study to date has linked ventral pathway activity with a behavioral measure indicating disruption of VWM storage.

To further evaluate whether ventral fronto-parietal cortex plays a role in disrupting VWM storage, the degree of feature overlap between the contents of VWM and visual distractors was manipulated. We examined activation elicited by visual distractors presented during the maintenance period of a visual change detection task (Luck and Vogel, 1997) across four conditions: no distraction, an abrupt visual onset, a distractor array containing within-category distractors, and a distractor array containing objects sharing features with the memory set. By manipulating the degree of similarity between memoranda and visual distractors we sought to modify the behavioral relevance of distractors and examine whether distractor-evoked processing along the ventral pathway is related to change detection performance.

## Methods

### Participants

Participants were 26 healthy, right-handed, English-speaking, Michigan State University undergraduate and graduate students (18 female), ages ( $M = 22.04$ , range = 19–28). Participants were paid for their participation in the study. The study was approved by the Michigan State University Office for the Protection of Human Subjects.

### Experimental procedure

#### Binding Change Detection Task

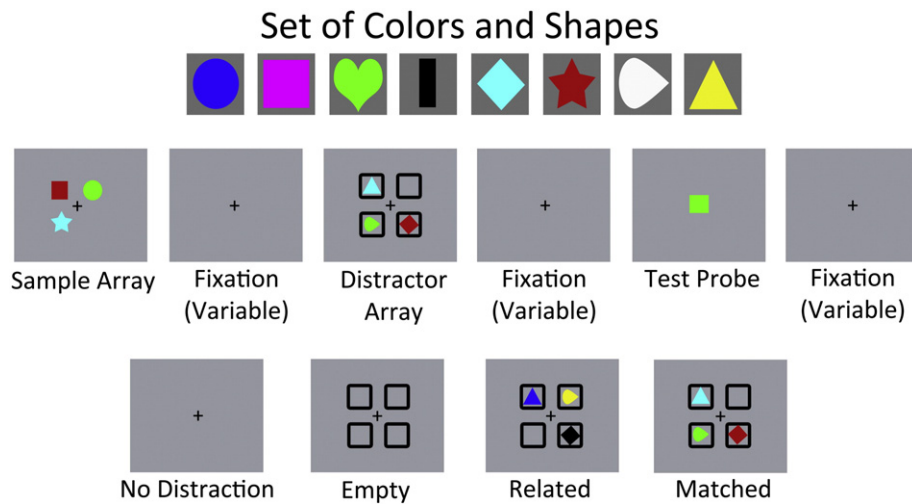
All stimuli were presented on a neutral gray background. Each trial began with the onset of a fixation cross to signal the beginning of a

trial (500 ms) immediately followed by the onset of 3 unique colored shapes presented around the corners of an invisible square centered on the screen for 1500 ms (“study array”). The exact corners of the invisible square at which the 3 objects appeared were randomly chosen on each trial. The invisible square occupied approximately  $11 \times 11$  degrees of visual angle (left-right and top-bottom) with each visual object measuring  $3.7 \times 3.7$  degrees of visual angle. After a variable fixation delay (2000–4000 ms jittered at 6 intervals) one of four distraction events was presented for 2000 ms: 1) No Distraction; 2) Empty array; 3) Related object array; and 4) Matched object array. In the No Distraction condition 2 s of fixation was included to match the duration of the other three conditions. In the Empty array condition empty boxes were presented, drawn in 5 pt black outline surrounding the location of study array objects. In the Related object condition the same black outline array was filled with 3 colored shapes generated from the same parent set of features as the study array but not matching any object in the study array on shape or color. In the Matched array the black outline box array was filled with 3 colored shapes generated from the same parent set of shapes as the study array, matching the study array objects in color but not matching in shape (each Matched distractor matched 1 object from the study array in color). In the Related and Matched conditions, distractor objects always appeared at 3 random locations within the array to make their onset location unpredictable.

After the offset of the distractor array, the fixation cross remained onscreen for a variable interval matched to the jittered pre-distractor fixation delay so that the total study to test interval was 8000 ms (e.g. pre-distraction fixation = 2000 ms + 2000 ms distractor array + 4000 ms post-distraction fixation). After the post-distraction array interval a single test object was presented centrally (presented directly over the fixation cross, center screen). The test object always included one shape and one color present in the study array. At test, participants judged whether the combination of shape and color in the test object was the ‘same’ as one of the objects at study or ‘changed’ across objects from study regardless of its original location in the study array (test object = 50% probability of same or changed). The test object remained visible for 2000 ms. After the offset of the test object the screen remained in solid gray background until the reappearance of the fixation cross signaled the beginning of the next trial (see Fig. 1).

Participants were instructed that the experiment was a test of visual memory and were provided with a visual depiction of each trial condition. The instructions included an emphasis on memorizing the combination of shape and color present in each study object, and that the test object would include one shape and one color that were both present in the study set. It was emphasized that participants respond as accurately as possible while attempting to make a response during the 2000 ms window while the test object was present on the screen. However, they were informed that on trials where they were not prepared to respond while the test object was visible, a response could still be made after the test object was cleared from the screen. They were urged to maintain fixation throughout the maintenance interval, and particularly while the distractor array was present. They were told that the goal of the study was to examine how well they could ‘mentally ignore the distractor array while the array was within their field of view.’ Thus, they were asked to not utilize alternative strategies such as closing their eyes or darting their eyes to an area of space outside the array. Upon debriefing all participants reported following these instructions and maintaining fixation throughout the maintenance interval.

Participants completed approximately 40 trials per condition ( $\pm 1$  trial per condition) for a total of 160 trials. The experiment was run in 10 blocks of 16 trials with a break between each block while the next fMRI scan was prepared. Trials of each distraction condition were randomly distributed within each run. Each run contained an equal number of trials (four) per distraction condition. Participants were in the scanner for a total of approximately 75 min including setup time, anatomical acquisition, between run breaks, and experimental runs. Eight colors and eight shapes constituted the parent set from which all stimuli



**Fig. 1.** fMRI task design. (Top) Example of all colors and shapes used to construct study objects. (Middle) time-course of each trial. (Bottom) Example of each distraction condition.

were generated including: white, black, yellow, cyan, blue, red, magenta, and green; circle, diamond, teardrop, tall rectangle, square, heart, triangle, and star (see Fig. 1). Prior to participation in the Binding Change Detection Task, participants were provided instructions and twenty practice trials with onscreen trial by trial feedback (correct/incorrect) to acquaint them with the experimental procedures. Additionally, participants were given a chance to ask any questions about the task and briefed on what to expect in the scanner environment (e.g. scanner noise during runs, how to use the response glove, and restricting head motion).

#### Behavioral analysis

Accuracy (corrected recognition rate, CR) was calculated separately for each condition (No Distraction, Empty, Related, and Matched) by subtracting the false alarm rate observed on unchanged (“same”) trials from the hit rate observed on change trials. Distraction-cost for each condition was defined as the difference in CR between each distractor condition and the No Distraction condition. For example, distraction-cost for the Matched object array condition was calculated by subtracting Matched CR from No Distraction CR, such that a higher distraction-cost was indicative of a greater loss of performance for the Matched object array condition as compared with the No Distraction condition.

#### Imaging data acquisition

MRI data acquisition was performed on a 3 T GE Signa Scanner. Functional data were collected with a Blood Oxygenation Level Dependent (BOLD) echo-planar imaging (EPI) sequence (TR/TE = 2000/27.7 ms, FOV = 220 mm, matrix = 64 × 64, slice-thickness/gap = 3.4/0 mm). For anatomical reference, registration of functional data, and for normalization of functional data to a standard T1 template (Montreal Neurological Institute, MNI) a T1 magnetization prepared, rapid-acquisition gradient echo (MPRAGE, TR/TE = 11.876/5.012 ms, FOV = 240 mm, matrix = 192 × 256, slice-thickness/gap = 1.5/0 mm) sequence was used to collect a high-resolution image of the participant's brain. Task stimuli were presented via E-Prime (version 2.0, Psychology Software Tools, Inc., Pittsburgh, PA) and projected from a shielded projector onto a screen mounted within the bore of the MRI scanner. The projector's image was reflected to the participant's visual field with a head-coil mounted mirror. Button-responses were logged with a BrainLogics Fiber Optic Response System glove (Psychology Software Tools, Inc., Pittsburgh, PA).

#### Imaging data preprocessing

fMRI and MRI data were preprocessed and analyzed using FMRIB's Software Library (FSL) fMRI Expert Analysis Tool (FEAT; Jenkinson et al., 2012). Functional data were brain-extracted, motion-corrected to the median functional image using b-spline interpolation (4 df), high-pass filtered (60 s/cycle), and spatially smoothed (9 mm full width at half maximum (FWHM), isotropic). The anatomical volume was brain-extracted and registered to the standard space T1 MNI template using tri-linear interpolation with FMRIB's Linear Image Registration Tool (FLIRT, 12 df). The median functional image was registered to the anatomical volume, and then transformed to the MNI template.

#### fMRI single-subject analysis (functional activation)

Statistical images were created using FEAT with an improved general linear model (GLM). Regressors were created by convolving binary time-course files containing the onset time for each condition with a canonical hemodynamic response function (double gamma HRF). Each single-subject model contained a regressor for each of the 4 conditions (No Distraction, Empty array, Related array, Matched array) at each stage of task performance (study, distraction, and test) resulting in 12 time-course regressors. Given our interest in the neural processes involved in disruption of VWM storage, all trials (accurate and inaccurate) were included in the analysis. Each regressor was entered into the GLM along with its temporal derivative and 6 motion parameters as nuisance regressors.

#### fMRI group analysis (functional activation)

In order to examine the effect of distraction condition on functional activation throughout the brain, a multiple linear regression form of repeated measures ANOVA was conducted separately for each stage of the task in FEAT. For each stage, subject-level statistical maps were entered into a second-level GLM along with an additional regressor per subject to account for subject-specific variance. Repeated measures ANOVAs on BOLD magnitude during study and test revealed no significant main-effect of condition. Therefore, only the results of the ANOVA on distractor activity are reported below. The repeated measures ANOVA results (beta-coefficient values) were Fisher-transformed to Z-values by the analysis package and thresholded at voxelwise FWE-corrected  $p < 0.05$ .

After identifying voxels exhibiting a significant main-effect of condition during the distraction period paired-samples contrasts were conducted in a second-level GLM in FEAT, restricted to voxels showing a whole-brain FWE-corrected  $p < 0.05$  main-effect of condition. For all within-subjects contrasts individual subject-level statistical maps were entered along with a regressor per subject to account for subject-specific variance (i.e. repeated measures). Results of paired-samples contrasts were Z-transformed and thresholded at voxelwise FWE-corrected  $p < 0.05$ .

#### Functional connectivity (fC) analysis

Significant relationships between BOLD magnitude in the right AI during the Related and Matched array conditions and distraction-costs during each condition were observed during the ROI analysis (see Results). To follow-up on these results a generalized form of the psychophysiological interaction (gPPI) model was implemented where we examined voxel-wise task-dependent functional connectivity with the right AI (McLaren et al., 2012). The gPPI model involved general linear modeling of the task conditions (psychological terms), the seed time-course (physiological term), and an interaction term for each task condition  $\times$  the seed time-course. Given no differences were observed between distraction conditions during study and test, study and test onsets were combined across distraction conditions into single study and test regressors per participant. The subject-level model for each participant included the following regressors: study, test, No Distraction (i.e. maintenance period without a distraction event), Empty array, Related array, Matched array, right AI seed time-course (Phys), study  $\times$  seed PPI, test  $\times$  seed PPI, No Distraction  $\times$  seed PPI, Empty array  $\times$  seed PPI, Related array  $\times$  seed PPI, and Matched array  $\times$  seed PPI.

To identify regions showing significant fC with the right AI during VWM maintenance in the absence of a distraction event a one-sample  $t$ -test was conducted on fC during the No Distraction condition. In addition, to examine changes in fC associated with each distraction array group-level repeated measures contrasts were conducted between distraction array conditions and the No Distraction condition, masked by the results of the one-way  $t$ -test on fC during the No Distraction condition. Masking the fC contrasts with the No Distraction restricted identification of changes in fC to regions showing significant connectivity in the absence of distraction. Similar to the contrasts conducted on functional activation, each within-subjects fC contrast was modeled in a second-level GLM by entering the subject-level statistical maps along with a regressor per subject to account for subject-specific variance. Due to the addition of multiple interaction terms, the gPPI model has less sensitivity to detect effects if they are present (McLaren et al., 2012). In order to reduce the likelihood of Type II error while simultaneously guarding against the increased likelihood of Type I error associated with a lower voxelwise threshold, a voxel-height plus clustering probability threshold (voxelwise  $p < 0.005$ ,  $k > 20$  voxels) was utilized to threshold the results of all fC analyses (Lieberman and Cunningham, 2009).

#### Region-of-interest (ROI) analysis

Mean percent signal-change for each ROI was generated using FSL's *featquery* utility. The location of each ROI was based on the results of the whole-group repeated measures ANOVA. To create an ROI mask image for each region a spherical mask was generated with a radius of 5 mm centered at the local peak identified within each cluster. The ROI masks were then registered back to native space where mean percent signal-change was calculated across all voxels falling within the spherical mask. Correlations between mean percent signal-change estimates and fC during distractor onsets and distraction-costs observed during test were performed in SPSS.

## Results

#### Corrected recognition (CR; hit rate minus false alarm rate)

A one-way repeated measures ANOVA was conducted on CR where a significant main-effect of condition was observed ( $F(3,75) = 7.39$ ,  $MSE = 0.09$ ,  $p < 0.0001$ ). Planned comparisons were conducted to reveal the shape of the main-effect of condition. While no significant reduction in CR was observed between Empty arrays and No Distraction ( $t(25) = -0.15$ ,  $p = 0.88$ ), a significant reduction in CR was observed between both Related and Empty arrays ( $t(25) = 2.52$ ,  $p = 0.02$ ) as well as Matched and Empty arrays ( $t(25) = 3.77$ ,  $p = 0.001$ ). No significant difference in CR was observed between Matched and Related ( $t(25) = 0.91$ ,  $p = 0.37$ ; see Fig. 2a).

#### Response time (RT)

The results of a one-way repeated measures ANOVA on mean RT to the test object revealed no significant main-effect of condition on RT ( $F(3,60) = 1.16$ ,  $MSE = 6497$ ,  $p = 0.33$ ). See Fig. 2b for mean RT per condition.

#### Whole-brain functional activation

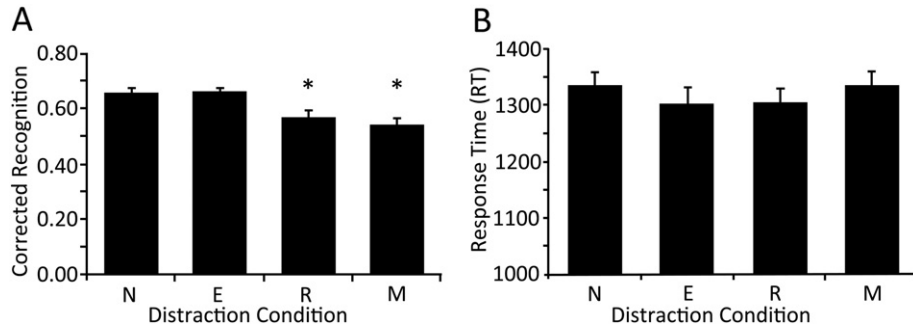
A whole-brain repeated measures ANOVA on activity during the distraction period revealed a significant main-effect of condition in frontal, parietal, visual, and ventral temporal regions of cortex, as well as several subcortical regions (see Fig. 3, top row). In order to examine the effect of each distraction condition four planned comparisons were performed: 1) Empty  $>$  No Distraction (the "onset-sensitive" contrast), 2) Related  $>$  Empty (the first "object-sensitive" contrast), 3) Matched  $>$  Empty (the second "object-sensitive" contrast), and 4) degree of memoranda-distractor overlap (Matched  $>$  Related). Significant voxels for the repeated measures ANOVA were those surviving a voxelwise threshold of FWE-corrected  $p < 0.05$  ( $Z > 4.0$ ).

A limited number of regions exhibited onset-sensitivity and no object-sensitivity. That is, they increased in activation to the onset of the Empty arrays and increased no further for object-filled arrays (primary visual cortex, left frontal pole; parahippocampal cortex/posterior thalamus; see Table 1; Fig. 3, middle row).

Regions of the superior parietal cortex including the vertex of the precuneus (SPL/Prec), the left and the right intraparietal sulci (IPS) as well as bilateral ventral occipital/inferotemporal (VO/IT) cortex exhibited both onset- and object-sensitive activation. At a slightly more liberal threshold of  $p < 0.001$ ,  $k > 10$  contiguous voxels the left IFG and left FEF, also displayed the same pattern of onset- and object-sensitivity. No regions showed increased activity during the inverse of each of these contrasts.

Comparison of the Matched  $>$  Empty and Related  $>$  Empty contrast results revealed that the Matched  $>$  Empty contrast entirely subsumed the Related  $>$  Empty contrast results (see Fig. 3, bottom row). To further examine the influence of similarity between distractors and the contents of VWM a contrast was performed between Matched and Related array conditions. The contrast of Matched  $>$  Related revealed that activity in the bilateral superior and inferior IPS, left IFG, SPL/Prec, and bilateral VO/IT cortex significantly increased between Related and Matched array conditions. Thus, a significant parametric increase in functional activation was observed in bilateral IPS, SPL/Prec, and bilateral VO/IT: Empty  $>$  No Distraction, Related  $>$  Empty, and Matched  $>$  Related (Fig. 4, left; Table 1). At the more liberal  $p < 0.001$  voxelwise threshold the left IFG and left FEF, similarly, exhibited such a parametric effect of distraction.

The results of the Matched  $>$  Empty and Related  $>$  Empty contrasts also revealed several regions that exhibited activation exclusive to object-filled distractor array conditions (i.e. no increase in activation to Empty arrays). These regions included the right TPJ, left and right



**Fig. 2.** Corrected recognition and RT for each condition. (A) A significant reduction in corrected recognition rate was observed between Empty and Related, and Empty and Matched arrays. No difference was observed between No Distraction and Empty or Related and Matched conditions. (B) No difference in RT was observed across any condition at test. N = No Distraction, E = Empty, R = Related, M = Matched.

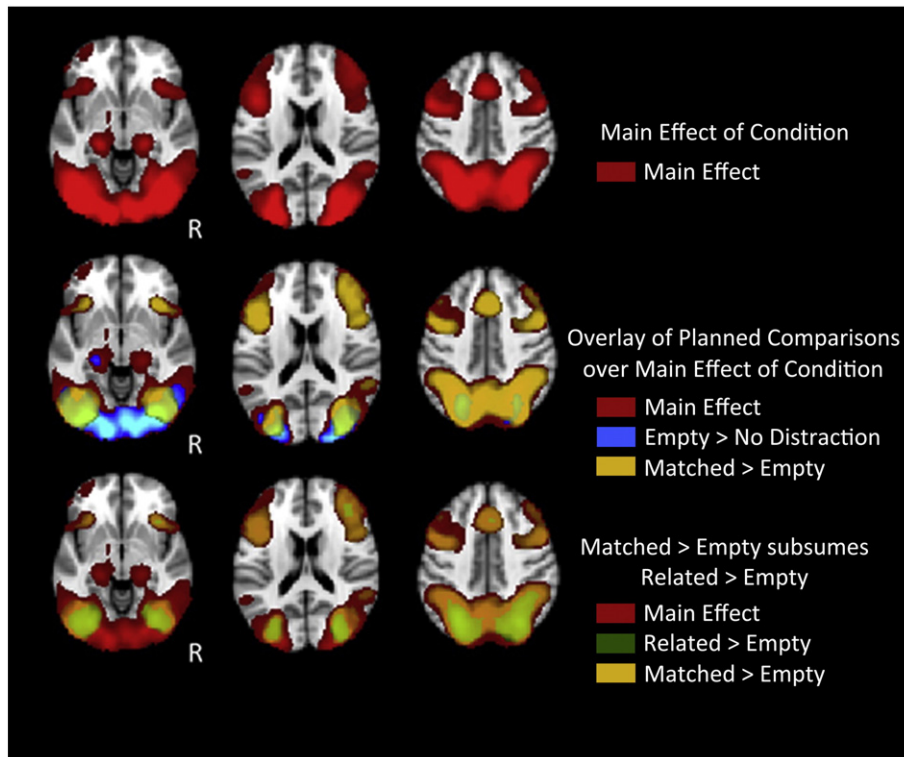
AI, right middle frontal gyrus (MFG), right FEF, ACC, and right IFG (see Fig. 4, right for percent signal-change among object-sensitive regions).

*ROI analysis on functional activation*

The right AI and right TPJ both exhibited profiles of activation that reflected performance on the change detection task, displaying only object-sensitivity, increasing in activation only during Related and Matched conditions. Right AI and Right TPJ ROIs were defined based on peak contrast results of Matched > Empty arrays (see above), allowing for an independent follow-up comparison test to be conducted on percent signal-change estimates during Empty arrays compared to No Distraction within these regions. Even at this more liberal ROI-based threshold, results of each paired *t*-test on percent signal-change confirmed that activation in the right AI ( $t(25) = 0.25, p = 0.81$ ) and

right TPJ ( $t(25) = -0.42, p = 0.68$ ) did not increase between No Distraction and Empty array conditions.

In addition, regions implicated in VWM storage (bilateral superior and inferior IPS; Todd and Marois, 2004, 2005; Xu, 2009; Xu and Chun, 2006) parametrically scaled in activation (significant at whole-brain voxelwise thresholds) with the degree of memoranda–distractor similarity. To further evaluate the role distractor-elicited activation in these ventral and dorsal regions played in disruption of VWM storage, brain–behavior ROI correlational analyses were conducted. These correlational analyses related activation during the distraction phase of the experiment to behavioral performance observed during the test phase, and thus were statistically independent of other analysis performed here and designed to examine whether activity to distractors could predict subsequent costs to performance at test (“distraction-costs” for Related and Matched trials = difference in CR between the No Distraction condition and each distractor condition).



**Fig. 3.** fMRI main-effect of distraction and planned comparisons. (Top) Regions showing a significant main-effect of condition during distractor onsets. (Middle) Results of planned comparisons between distractor conditions overlaid the main-effect of condition. (Bottom) Results of the contrast Matched > Empty overlaid the results of Related > Empty.

**Table 1**  
Results of whole-brain analysis and contrasts between conditions during maintenance.

Region	Peak of ME			Onset-sensitive	Object-sensitive	Para	ME	E > ND	R > E	M > E	M > R
	X	Y	Z								
Left hemisphere											
Frontal											
FEF	−36	4	50	X*	X	X*	7.41	3.26*	3.51*	5.09	3.44*
IFG	−44	4	30	X*	X	X*	8.88	3.43*	3.55*	6.15	4.39
AI	−34	22	−4		X		5.87	−	3.29*	4.94	−
Frontal pole	−42	50	−16	X			4.94	4.26	−	−	−
Parietal											
Superior IPS	−12	−70	48	X	X	X	9.24	4.43	4.23	5.88	4.39
Inferior IPS	−28	−70	28	X	X	X	9.75	4.04	5.49	6.56	5.16
Occipital											
Lateral VO/Inferotemporal	−42	−68	−16	X	X	X	11.06	5.35	6.21	7.17	5.71
Primary visual cortex	−10	−94	−8	X			9.87	6.39	−	−	−
Midline											
ACC	0	20	46		X		7.77	−	4.23	6.08	3.59*
SPL/Precuneus	−2	−64	50	X*	X	X	9.28	4.03	4.06	6.19	4.55
Sub-cortical											
R Thalamus	20	−30	−6	X*			7.01	3.74*	−	−	−
L Thalamus	−20	−30	−6	X			7.17	4.34	−	−	−
L Pallidum	−14	−2	−4				4.5	−	−	−	−
Right hemisphere											
Frontal											
FEF	30	4	52		X		6.31	−	3.16*	5.07	3.46*
IFG	42	8	28		X		7.72	−	−	5.43	4.00*
MFG	40	32	24		X		6.44	−	4.22	5.18	−
AI	36	22	−6		X		6.35	−	4.15	5.34	−
Parietal											
Superior IPS	12	−70	52	X	X	X	10.4	4.74	4.93	6.58	4.58
Inferior IPS	32	−70	26	X	X	X	10.01	4.31	5.39	6.95	4.74
TPJ (R Ang)	54	−46	28		X		6.02	−	3.37*	5.47	3.57*
Occipital											
Lateral VO/Inferotemporal	40	−68	−18	X	X	X	11.7	5.27	6.28	7.27	4.57
Primary visual cortex	8	−90	−12	X			10.65	7.20	−	−	−

Note: Coordinates are in MNI space, ME = Z-value for main-effect of distraction condition, M = Matched, R = Related, E = Empty, ND = No distraction, \* = reliable at  $p < 0.001$ , uncorrected for multiple comparisons. Para = regions showing a parametric increase in activation across distractor classes. Coordinates under "Peak of ME" are the local maximum from the main-effect of distraction condition. Z-values reported under each contrast reflect the respective contrast Z-stat at the coordinate listed under "Peak of ME".

No significant brain–behavior correlation was observed in the left or right IPS, or the right TPJ for either distraction condition (all  $p$ 's > 0.1). Significant positive correlations were observed in the right AI between activation elicited by Related and Matched distractors and respective distraction-costs (Empty:  $r = 0.3$ ,  $p > 0.1$ ; Related:  $r = 0.5$ ,  $p = 0.01$ ; Matched:  $r = 0.42$ ,  $p = 0.03$ ; Fig. 5).

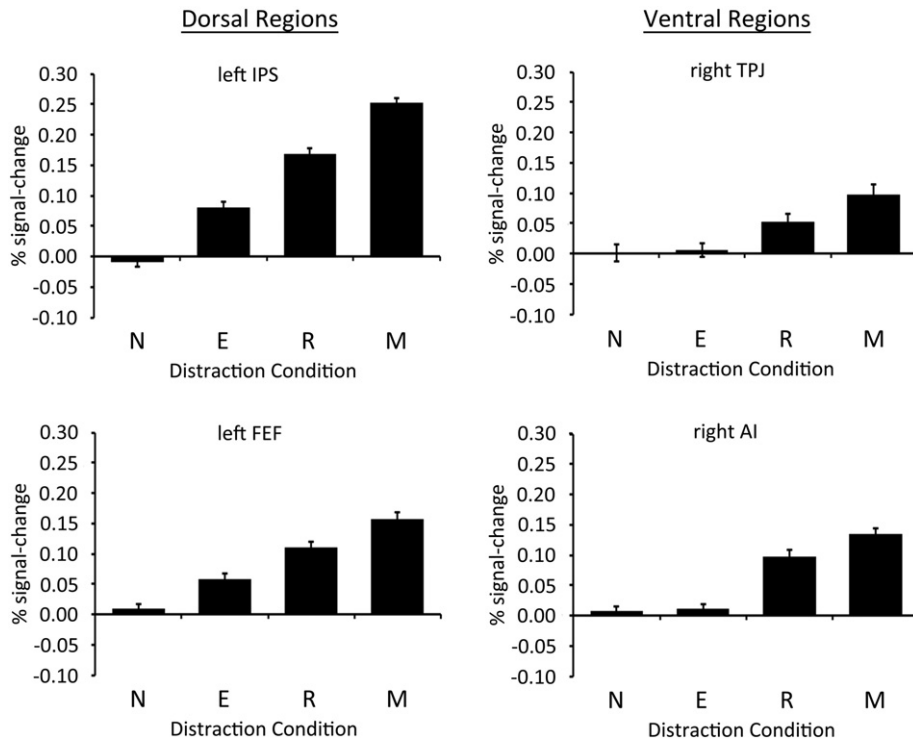
#### Right AI functional connectivity (fC) analysis

The two-network model of attentional control suggests that the ventral fronto-parietal network contributes a reorienting signal to the dorsal network in the presence of behaviorally relevant information in order to dynamically modulate goal-directed behavior (Corbetta et al., 2008; Greene and Soto, 2014; Han and Marois, 2013; Serences et al., 2005). Results of our activation and brain–behavior correlation analyses indicated that activation in the right AI during distractor onsets reflected change detection performance and predicted individual differences in distraction-costs observed at test during Related and Matched array conditions. In order to examine whether right AI activity contributed to distraction-costs by modulating ventral–dorsal connectivity, a functional connectivity analysis was conducted based on the seed time-course of the right AI.

The results of a one-way  $t$ -test on fC during No Distraction revealed that the right AI was functionally connected with regions implicated in VWM storage, bilateral IPS and bilateral VO/IT cortices, during VWM maintenance (Fig. 6, top left). Functional connectivity of these regions was reduced during both Related and Matched array onsets

compared to No Distraction. There were differences, however, in the pattern of connectivity disruption observed between Related and Matched conditions. Results of the fC contrast between the Related array and No Distraction revealed that the onset of Related distractors resulted in a significant reduction in fC between the right AI, left inferior IPS, and left VO/IT cortices. In contrast, the onset of Matched arrays was associated with a significant reduction in fC between the right AI and bilateral inferior and superior portions of the IPS (Fig. 6, bottom left).

To further characterize changes in fC during Related and Matched distractor onsets fC–behavior relationships were explored between regions showing reduction in fC during each distraction condition and respective distraction-costs. During Related arrays no significant relationships were observed between fC in the right VO/IT cortex (−44, −68, −6) and right inferior IPS (−27, −74, 26) and distraction-cost (both  $p$ 's > 0.23). Among the four regions showing reduced fC with the right AI during Matched arrays (bilateral inferior and superior IPS), a significant positive correlation was observed between Matched distraction-cost and fC with the right superior IPS (28, −60, 44;  $r = 0.42$ ,  $p = 0.03$ ) and a marginal positive correlation was observed between Matched distraction-cost and fC with the left superior IPS (−28, −52, 42;  $r = 0.36$ ,  $p = 0.07$ ). Thus, greater connectivity between these regions was associated with greater effects of distraction on memory performance. No relationship between fC and Empty or Related distraction-costs were observed in these regions (all  $p$ 's > 0.1). See Fig. 6, top right for a graph of connectivity strength between the right AI and the right superior IPS during each distraction condition.



**Fig. 4.** Activation profiles for dorsal and ventral fronto-parietal regions. Percent signal-change estimates from within ROIs showing a main-effect of distractor condition. All plots are only for display and represent the activation profiles of significant effects observed at voxel-wise FWE-correct  $p < 0.05$ . (Left) Voxelwise planned comparisons revealed several fronto-parietal regions displaying both onset- and object-sensitivity, including the left FEF. A subset of these regions, including bilateral IPS, scaled parametrically in activation from No Distraction to Empty, Empty to Related, and Related to Matched. (Right) Ventral fronto-parietal regions increased in activation exclusively during Related and Matched array onsets. N = No Distraction, E = Empty, R = Related, M = Matched.

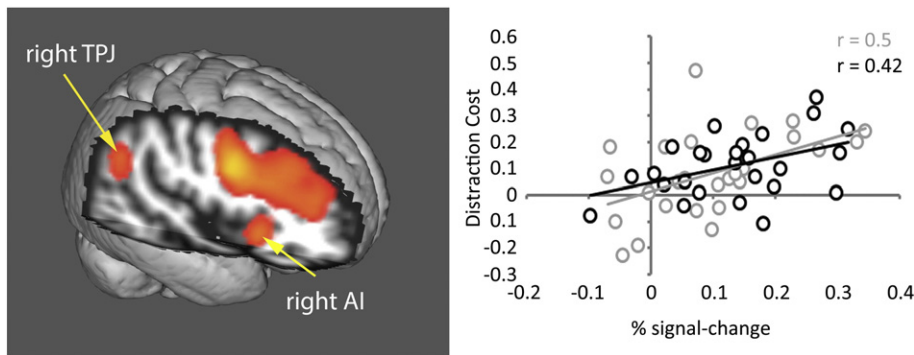
*Summative contributions of activity and fC to matched distraction-costs*

Activation in the right AI and fC between right AI and right sIPS was not correlated ( $r = -0.05, p = 0.80$ ), raising the possibility that each made separable contributions to Matched distraction-costs. Step-wise multiple linear regression modeling was performed to investigate the unique contributions of right AI activation and fC between the right AI and right superior IPS to Matched distraction-costs. Activation in the right AI was obtained from the initial GLM on functional activation, and fC between right AI and right superior IPS was obtained from the gPPI model in which connectivity was estimated independently from (i.e. controlling for) the contribution of task-related activation in this region. Alone, activation in the right AI accounted for 17.4% of the variance in Matched distraction-costs ( $B = 0.42, p = 0.03$ ). Connectivity between right AI and right superior IPS accounted for an additional

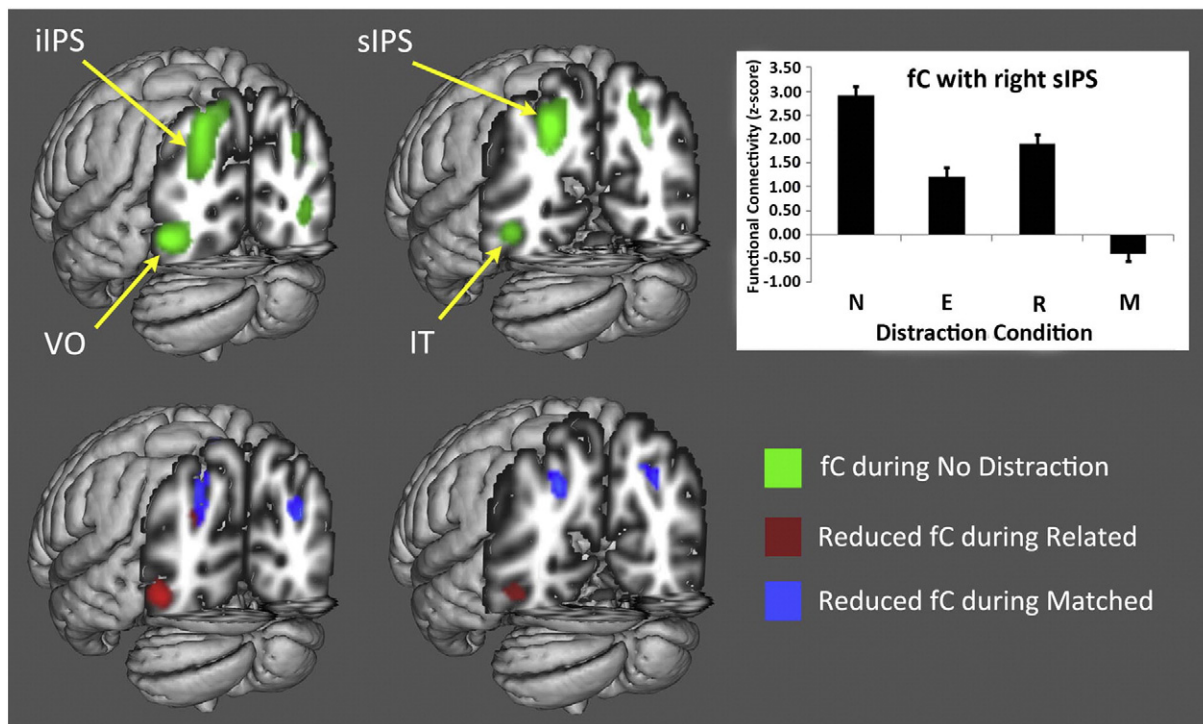
19.2% of the variance in Matched distraction-cost ( $F\text{-change}(1,23) = 6.96, p = 0.02; B = 0.44, p = 0.02$ ). Together, the combined activity and fC model exhibited good fit ( $F(2,23) = 6.64, \text{MSE} = 0.06, p = 0.005$ ) and accounted for 36.6% of the total variance in Matched distraction-costs.

**Discussion**

Our current results expand our knowledge of how visual distractors are processed across regions of fronto-parietal cortex during VWM maintenance and suggest that task-related VWM distractors affect storage through processing along a ventral fronto-parietal pathway. The present study provides several novel findings concerning VWM distraction including evidence that: 1) activation of the right AI is selective to behaviorally relevant distractors during VWM maintenance and is



**Fig. 5.** Activation of right AI during distractor onset correlated with distraction-costs at test. (Left) Sagittal view of the Matched > Empty contrast showing the right TPJ and right AI. (Right) Distraction-costs to binding change detection was predicted by activation in the right AI during Related (gray) and Matched (black) distractor array onsets.



**Fig. 6.** Distractor Objects differentially disrupted fronto-parietal functional connectivity. (Top left) Functional connectivity (fc) between the right AI and bilateral IPS and VO/IT cortices was observed in absence of distraction (shown in green). (Bottom left) Related distractor objects significantly reduced connectivity between the right AI and left inferior IPS and left VO/IT cortices (shown in red). Matched distractor objects significantly reduced connectivity between the right AI and bilateral inferior and superior IPS (shown in blue). (Top right) Graph of connectivity strength between the right AI and the right superior IPS during each distraction condition. Note: No significant difference in fc was observed between No Distraction and Empty conditions and Empty and Related conditions (both  $p$ 's > 0.26). N = No Distraction, E = Empty, R = Related, M = Matched, sIPS = superior intraparietal sulcus.

predictive of subsequent behavioral costs to VWM performance at test, 2) memoranda–distractor similarity affects connectivity between ventral and dorsal networks differentially depending on the degree of memoranda–distractor similarity, and 3) greater connection between ventral frontal and superior parietal cortices during distractor onsets is associated with greater costs to VWM performance.

The disruption to change detection performance associated with Related and Matched distractor objects was reflected in the pattern of activation observed across ventral fronto-parietal cortices. Ventral regions did not activate during the onset of Empty arrays despite their abrupt and unpredictable onset timing throughout the task. This observation is consistent with the behavioral relevance theory of ventral attention network function advanced by neuroimaging research on selective visual attention (de Fockert et al., 2004; Kincade et al., 2005; Serences et al., 2005). During visual search tasks ventral network regions have been shown to preferentially respond to distractors that share features with the target of search (Serences et al., 2005). Here we observed a similar pattern where activity for task-irrelevant onsets (i.e. Empty arrays) in ventral network regions was equivalent to activity when no distraction was present, and increased only when arrays were filled with objects related to the contents of VWM. This pattern of ventral fronto-parietal activation, along with the observation that increases in right AI activation were associated with greater costs to VWM performance, suggests that disruption of VWM storage may occur through a behavioral relevance mechanism.

Recent work has focused on delineating the functional roles played by two major nodes of the ventral network, the right TPJ and the right AI (Greene and Soto, 2014; Han and Marois, 2013; Shulman et al., 2009). Current evidence suggests that while both regions are sensitive to attention arresting information, the right TPJ may play more of an evaluative role where the right AI may integrate with other functional networks to reorient attention (Greene and Soto, 2014; Han and

Marois, 2013; Shulman et al., 2009). In particular, Han and Marois (2013) recently demonstrated that the activation profile of the right AI, among several ventral network regions active during an oddball task, was most consistent with the pattern that would be expected from a brain region involved in the reorienting of attention, activating transiently during the onset and offset of salient visual stimuli. Our current results advance this interpretation by showing that activation of the right AI was more directly associated with disruption of goal-directed cognition (maintenance of information in VWM) than the right TPJ.

Deactivation of the ventral network, specifically the TPJ, has been linked to successful VWM encoding (Anticevic et al., 2010a,b), VWM load, and a lack of awareness of transient visual events during VWM maintenance (Todd and Marois, 2005). For example, Anticevic et al. (2010a, 2010b) observed greater deactivation of the right TPJ during the study phase of their VWM task, and activity of this region was associated with higher accuracy during test. Activity of this region increased during the maintenance interval in which distraction was present but there was no relationship of brain activity to distractors and VWM performance in their study. Similarly, we observed activation in the right TPJ and right AI during distractor onsets after encoding had been completed. Moreover, activation of the right AI during Related and Matched arrays consequently predicted reduced change detection accuracy at test. Taken together, these results suggest that ventral attention network regions may operate as part of a give-and-take mechanism between internally- and externally-directed attention during VWM storage processes, deactivating to facilitate the internal allocation of attention toward VWM processing and activating to return attention externally to the environment (Kiyonaga and Egner, 2012). However, future research is required to determine if this relationship reflects the influence of attention over VWM storage.

Dorsal regions of fronto-parietal cortex responded to the onset of each distraction array in a manner suggesting that similarity between



internally maintained objects and external stimuli plays a role in the recruitment of control over VWM distraction. Empty arrays contained no behaviorally relevant features, but demarcated the set of locations that study objects were displayed throughout the task. Consistent with previous evidence, the abrupt onset of Empty arrays resulted in increased activation across dorsal regions compared to trials without distraction (Dolcos et al., 2007; Jha et al., 2004). Theories of attention and working memory suggest that dorsally situated fronto-parietal regions are involved in top-down control over cognitive processing (reviewed in Corbetta et al., 2008; Gazzaley and Nobre, 2012; Postle, 2006; Yantis, 2008). Accordingly, the difference in activation elicited between Empty, Related, and Matched object arrays may reflect the overall higher level of difficulty in processing distractor objects with increasing similarity to the contents of VWM.

Our current results show that the degree of overlap (categorical overlap/categorical + feature overlap) between memoranda and visual distractors has a bearing on both dorsal fronto-parietal recruitment and connectivity. While the pattern of regions activated by Related and Matched distractors did not dissociate between distractor objects, the results of our fC analysis revealed that these distractors differentially affected functional connectivity between ventral and dorsal networks. The right AI was connected in the absence of distraction with regions of bilateral IPS and VO/IT regions that were significantly activated by distractors. Previous work has shown that the IPS and VO/IT cortices play a central role in VWM storage, tracking parametrically with the number of objects estimated to be held in VWM (Mitchell and Cusack, 2008; Song and Jiang, 2006; Todd and Marois, 2004; Xu and Chun, 2006). However, the functional roles of the superior and inferior IPS are dissociable with the inferior IPS tracking with the number of objects maintained in VWM and the superior IPS tracking with the complexity (in terms of density of features) of objects maintained (Xu, 2008; Xu and Chun, 2006).

The pattern of our current fC results shows that modulations of ventral-dorsal connectivity may be selective to the level at which distractors overlap with the objects maintained in VWM, with both types of *objects* modulating inferior IPS connectivity and only objects with matching *features* modulating superior IPS connectivity. While representations stored in VWM have been decoded from activation in extrastriate cortices (Ester et al., 2009; Harrison and Tong, 2009; Serences et al., 2009), recent classification evidence suggests that VWM storage may be redistributed to the IPS as a means to avoid interactions between VWM representation and newly perceived information (Bettencourt and Xu, 2014). In a recent study by Bettencourt and Xu (2014), objects stored in VWM could be decoded through pattern classification on activation in visual cortices when participants knew distractors were not imminent in a given trial. However, when participants were cued to expect distractors object representations could only be decoded from activity in the IPS (Bettencourt and Xu, 2014).

If VWM representations are indeed distributed to the IPS when distractors are highly likely, the connectivity pattern observed in our current study may reflect the action of a fronto-parietal gating/updates mechanism (see also McNab and Klingberg, 2008). Unlike the phasic circuit-breaker analogy used to describe the role of the right TPJ in orienting processes (Corbetta et al., 2008; Todd et al., 2005) the right AI may maintain a sustained connection with dorsal parietal regions in the absence of distraction in order to rapidly adjust goal-directed behavior, updating VWM when new relevant information is present in the environment. Disconnecting in the presence of behaviorally relevant information that is potentially distracting (as was observed here) would therefore serve an important role in protecting against loss of VWM representations. This interpretation, however, is only a speculation at this point. What can be said is that greater connection between ventral and dorsal networks during Matched distractor onsets was associated with increased disruption of VWM performance. This result points to disconnection between networks in the presence of salient visual information as a means to protect the contents of VWM.

Previous studies of VWM distraction have shown that objects from the same category as the memoranda (e.g. face distractors during VWM for faces) are more disruptive and elicit greater cortical recruitment than objects from different semantic categories (e.g. places; Dolcos et al., 2007; Jha et al., 2004; Yoon et al., 2006; Anticevic et al., 2010a,b). These previous findings suggest that memoranda-distractor similarity affects VWM performance and the recruitment of cognitive control during VWM storage (Gazzaley and Nobre, 2012; Jha et al., 2004; Yoon et al., 2006). However, to date, brain imaging studies of distraction during VWM storage have only examined the influence of categorical-overlap between visual distractors and internally maintained objects on performance and control. One of the key challenges of systematically investigating other forms of similarity, e.g. feature-overlap, is constructing distractors that match internally maintained objects without replicating the study objects (see perceptual resampling in Soto et al., 2007; Woodman and Luck, 2007). The binding change format of the change detection task utilized here (see also Johnson et al., 2008; Wheeler and Treisman, 2002) examines memory for feature associations within study objects (as opposed to the in/out of memory format of single feature change detection; e.g. Luck and Vogel, 1997) and allows for control over partial feature-overlap between study and distractor objects without presenting studied objects as distractors. Accordingly, this format eliminates the risk of participants sampling distractor objects in order to reinforce the studied feature bindings.

Our current study was designed to examine whether the dynamics of the two-network theory of attentional control, based on studies of visual search, would be similarly reflected in distractor processing during VWM storage. It is important to note, especially given the likely involvement of cognitive control mechanisms during distractor processing, that the dorsal and ventral fronto-parietal regions observed in our results may neighbor or overlap with other well-described functional networks involved in task/cognitive control processes and multi-sensory integration. Regions surrounding opercular cortex (anteriorly, the AI and posteriorly, the TPJ) are often active during tasks that involve multimodal binding operations (Sterzer and Kleinschmidt, 2010; Cabeza et al., 2012). Therefore, an alternative account of our findings may suggest that instead of a behavioral relevance orienting signal, activation of the right AI and right TPJ may reflect the binding of new information during distraction, and perhaps replacement of information in VWM (Ueno et al., 2011).

In addition, a multi-network theory of task control advanced by Petersen, Posner, and colleagues suggests that the orienting networks described by Corbetta and colleagues closely neighbor the cingulo-opercular and fronto-parietal task control networks as well as the salience network (Menon and Uddin, 2010; Petersen and Posner, 2012; Power and Petersen, 2013). Recent evidence suggests that the task control networks may contribute control signals at independent timescales (sustained and phasic, respectively) and exhibit patterns of activation similar to what we observed in our current results (i.e. increase in activation with increasing demand for top-down control; Dosenbach et al., 2006; Dosenbach et al., 2007). Our current design may not be entirely capable of adjudicating between orienting and task control accounts; however, the results of our connectivity analysis show that the two networks were more connected in the absence of distraction than the task control network theory would suggest (Power and Petersen, 2013).

Of relevance to our current results, bilateral anterior insula and anterior cingulate cortex are thought to constitute the salience network. Activation of the salience network is frequently observed in tasks that involve personally relevant, emotional, or threatening stimuli (Menon and Uddin, 2010). While stimulus classes such as threatening stimuli may not share any features with the current working memory task, they may be regarded as highly relevant and expected to engage regions that were not activated by the Empty arrays here, such as the right AI. Findings such as these would have important implications for the definition of behavioral relevance and theories involving the ventral attention network. We suggest that future research could include additional

manipulations such as warning cues, varying VWM loads, and additional distractor classes in order to examine the influence and/or interaction of large scale control, orienting, and salience networks during VWM processing.

An additional caveat to our current findings also warrants further consideration. Related objects contained visual features that were studied regularly throughout the course of the experiment and, given the limited number of features in the parent set, often contained features that were studied on a previous trial. Thus, while they did not directly match the current contents of VWM, they did match regularly (and often recently) active features in VWM. The regularity with which these features were studied may have influenced their relevance and resulted in a form of a proactive interference effect on change detection performance (see “recent probes” effect in Jonides and Nee, 2006; Makovski and Jiang, 2008). Similarly, Related distractor objects (“plausible suffixes” in Ueno et al., 2011) were shown to selectively disrupt binding change detection performance compared to task irrelevant objects, suggesting that such objects are more difficult to filter before reaching VWM than task irrelevant objects. In future studies the frequency with which lag-1 study objects appear as distractor objects could be manipulated to further investigate the potential role that proactive interference plays in distraction of VWM storage.

## Conclusions

Our current results show that disruption of VWM involves processing in ventral fronto-parietal regions involved in the stimulus-driven control of attention. The current study provides novel evidence that functional connection between ventral and dorsal networks during distraction plays a role in disrupting VWM storage. Our study provides further support for integrated neural theories of attention and working memory, and should serve as a gateway for further investigations into the role memoranda-distractor feature-overlap plays in the control of attention and visual working memory.

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