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Perceptual Coupling and Decoupling are Associated with Individual Differences in Working Memory Encoding and Maintenance

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Abstract

Working memory (WM) allows goal-relevant information to be encoded and maintained in mind, even when the contents of WM are incongruent with the immediate environment. While regions of heteromodal cortex are important for WM, the neural mechanisms that relate to individual differences in the encoding and maintenance of goal-relevant information remain unclear. Here, we used behavioral correlates of two large-scale heteromodal networks at rest, the default mode (DMN) and frontoparietal (FPN) networks, to understand their contributions to distinct features of WM. We assessed each individual's ability to resist distracting information during the encoding and maintenance phases of a visuospatial WM task. Individuals with stronger connectivity of DMN with medial visual and retrosplenial cortex were less affected by encoding distraction. Conversely, weaker connectivity of both DMN and FPN with visual regions was associated with better WM performance when target information was no longer in the environment and distractors were presented in the maintenance phase. Our study suggests that stronger coupling between heteromodal cortex and visual-spatial regions supports WM encoding by reducing the influence of concurrently presented distractors, while weaker visual coupling is associated with better maintenance of goal-relevant information because it relates to the capacity to ignore task-irrelevant changes in the environment.

Key words: default mode; distractor; frontoparietal; intrinsic connectivity; resting-state.

Introduction

Working memory (WM) allows us to hold information actively in mind (Baddeley and Hitch 1974; Baddeley 1983; Baddeley 1992) and supports multiple facets of complex behavior including the ability to learn about and comprehend the world around us and to perform numerical calculations and reasoning tasks (Waltz et al. 1999; Geary et al. 2004; Gathercole et al. 2019). It also provides the workspace in which naturally occurring spontaneous thoughts emerge, especially those with social episodic features (Teasdale et al. 1993; Teasdale et al. 1995; Smallwood et al. 2009; Smallwood et al. 2013; Turnbull, Wang, Schooler, et al. 2019; Turnbull, Wang, Murphy, et al. 2019). The behavioral flexibility that WM conveys is thought to depend on two distinct processes: this system's capacity to encode goal-relevant information during period of external focus (Myers et al. 2017; Lewis-Peacock et al. 2018; Van Ede et al. 2019) and its role in maintaining internal representations with current relevance even as the external world changes (Konstantinou et al. 2014; McNab and Dolan 2014; Lorenc et al. 2021). It

has been argued that the ability to encode appropriate information in the environment depends on a process of attentional control that allows task-relevant material to be encoded and distractions to be suppressed (Gazzaley et al. 2005), while the maintenance of these representations may depend on the ability to decouple cognition from the external environment, reducing the interference between the ongoing mental content and incongruent external information (Smallwood 2013).

Individual differences in distractor resistance ability are strongly predictive of WM capacity, which varies substantially between individuals (Vogel et al. 2005; McNab and Dolan 2014; Feldmann-Wüstefeld and Vogel 2019). Moreover, resistance to interference is thought to draw on externally and internally oriented cognitive processes during encoding and maintenance, respectively: the ability to ignore task-irrelevant distracting information presented together with target information during encoding and the capacity to maintain information in mind during a delay while irrelevant information is presented (McNab and Dolan 2014; McNab et al. 2015). These components vary independently across individuals; they both make

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a *unique* contribution to WM capacity while controlling for performance in the absence of distraction (McNab and Dolan 2014), consistent with the view that separable neurocognitive mechanisms underpin these aspects of WM capacity.

It is widely recognized that regions of heteromodal cortex in the prefrontal and parietal cortex are important for WM (Veltman et al. 2003; McNab and Klingberg 2008; Gazzaley and Nobre 2012). For example, regions of the frontoparietal control network (FPN) are implicated in the maintenance of current goals (Cole et al. 2013) and support the top-down regulation of sensory processing to aid selective encoding and maintenance of goal-relevant information (Curtis and D'Esposito 2003; Gazzaley and D'Esposito 2007; Gazzaley and Nobre 2012). Activation of this control network increases with the amount of to-be-remembered information (Braver et al. 1997; Manoach et al. 1997; Jansma et al. 2000; Veltman et al. 2003; Narayanan et al. 2005), and it functionally couples with visual regions that selectively process relevant information during the encoding of visual inputs (Chadick and Gazzaley 2011). Prefrontal control regions are also implicated in the active maintenance of target information in the face of irrelevant distractors (Roberts et al. 1994; Chao and Knight 1998; Sakai et al. 2002; Jha et al. 2004; Feredoes et al. 2011; Konstantinou et al. 2014; Robison et al. 2018), and they are active when participants anticipate maintaining relevant information in WM while ignoring irrelevant information in the environment (McNab and Klingberg 2008). In addition, the functional decoupling of control sites from the sensory cortex during WM maintenance could minimize interference from irrelevant stimuli (Clapp et al. 2010).

More recently, studies have implicated the default mode network (DMN) in situations that depend on WM (for a review, see Smallwood et al. 2021). For example, the DMN has a well-established role in spontaneous thought (Mason et al. 2007; Christoff et al. 2009), when attention is focused on input from memory (Poerio et al. 2017; Wang et al. 2020) and the cortical processing of information from the external environment is reduced (Smallwood et al. 2008; Kam et al. 2011; Baird et al. 2014). Moreover, the DMN is associated with task situations in which memory can guide cognition, such as the application of task rules and information from previously presented stimuli (Crittenden et al. 2015; Vatansever, Menon, et al. 2017; Murphy, Wang, et al. 2019; Wang, Gao, et al. 2021). Earlier studies showed that the DMN is often anticorrelated with regions implicated in cognitive control (Fox et al. 2005)—and this pattern is associated with better performance on challenging externally presented tasks (Lawrence et al. 2003; McKiernan et al. 2003; Āeko et al. 2015; Hearne et al. 2015). However, both DMN and FPN can exhibit greater activation when decision-making depends on the retrieval of information from memory, in comparison to judgments made on the basis of perceptual input; moreover, better 1-back performance is associated with increased DMN activity,

relative to 0-back performance (Spreng et al. 2014; Konishi et al. 2015; Murphy et al. 2018; Murphy, Wang, et al. 2019). These findings suggest a role of DMN in internal memory representation, which might be relevant to both the formation and maintenance of the contents of WM. In line with this view, a recent study revealed the functional role of this network in the maintenance of goal-relevant information in a semantic task (Wang et al. 2021), and studies have also shown DMN works together with control regions to support goal-directed WM tasks (Spreng et al. 2010; Elton and Gao 2015; Hearne et al. 2015; Piccoli et al. 2015; Vatansever, Manktelow, et al. 2017). For example, one study found an anticorrelation between the DMN and control regions only during the maintenance phase of WM in the absence of external input, and functional coupling between these networks during both encoding and retrieval phases of WM (Piccoli et al. 2015). DMN regions can also increase their connectivity with control regions to support increasing cognitive demands (Vatansever, Manktelow, et al. 2017); moreover, stronger coupling of DMN regions with other DMN and visual regions is linked to better WM performance (Hampson et al. 2006; Vatansever, Manktelow, et al. 2017).

The capacity of these heteromodal networks to be perceptual coupled and decoupled might be a key feature of WM: The functional coupling with perceptual systems might enable the selective encoding of goal-relevant information, while perceptual decoupling might be important for the maintenance of these internal representations, since it has been argued that perceptual decoupling helps to reduce the interference from external inputs (Smallwood 2013). In the current study, we therefore used functional neuroimaging to examine the neurocognitive mechanisms that contribute to individual differences in distractor resistance ability in visuospatial WM, focusing on the role of heteromodal cortex and the patterns of coupling and decoupling it can form with the visual cortex. The task design is described in (Fig. 1). In brief, participants were asked to remember the positions of target stimuli presented with or without distractors, to hold this information in mind, and then decide whether a target had been shown in the position indicated by a question mark or not. Distractors were either presented simultaneously with the targets during the encoding phase of the WM task or during the maintenance phase, after the targets disappeared. Contemporary evidence suggests that heteromodal systems exert their influence on cognition in part through their links to other regions of cortex, including sensory systems (e.g., Smallwood 2013; Zhang et al. 2019; Li et al. 2021). Accordingly, our study aimed to delineate the neural basis of individual differences in the ability to hold goal-relevant information in mind in the face of distraction. We tested four intersecting hypotheses: 1) individual differences in the connectivity of heteromodal systems will relate to differences in distractor resistance in the WM task; 2) these effects might not be restricted to FPN,

associated with cognitive control, but might extend to DMN given emerging evidence of the role of this network in memory-guided cognition; 3) connectivity of these heteromodal systems might relate to encoding and maintenance phases of the task in different ways; and 4) more specifically, sensory coupling and decoupling of FPN and/or DMN may separate these task stages. The ability to encode relevant information may be associated with stronger perceptual coupling of heteromodal cortex while the maintenance of information in WM during the presentation of irrelevant information in the external world may depend on the capacity of FPN and/or DMN to function independently of external input. In this way, our study aimed to extend our understanding of individual differences in the ability to hold goal-relevant information in mind.

Materials and Methods

Participants

In all, 135 undergraduate and postgraduate students were examined in this study (age range 18–25 years, mean age \pm standard deviation (SD) = 20.92 \pm 2.45, 56 males). All were right-handed native English speakers and had normal or corrected-to-normal vision. None of them had any history of neurological impairment, diagnosis of learning difficulty, or psychiatric illness. All provided written informed consent prior to taking part and received a monetary reward for their participation. No power calculation was performed to determine this sample size; instead, all usable data from an existing dataset were included in the analysis. Data from three participants were removed due to excessive head motion (i.e., mean head motion >0.4 mm). The final sample therefore consisted of 132 participants. In this study, participants took part in a resting-state scan and on subsequent days completed a battery of questionnaires and tasks focusing on memory and mind-wandering, which were outside the scope of this study (e.g., Wang et al. 2017; Vatansever, Bzdok, et al. 2017; Zhang et al. 2019). Ethical approval was obtained from the Research Ethics Committees of the Department of Psychology and York Neuroimaging Centre, University of York, and all research was performed in accordance with the relevant guidelines/regulations.

Behavioral Assessment

The experiment consisted of one session of a computer-based WM task previously used by McNab and Dolan (2014). Participants were asked to remember the positions of three red circles (target stimuli) presented on a circular grid of 16 squares, with or without distraction (two yellow circles), and respond to a probe stimulus (a question mark) which asked them to indicate whether a red target circle had been shown in the position indicated (a yes/no response). The session included three conditions, with 30 trials of each condition presented in

pseudorandom order. In the No Distraction (ND) condition (Fig. 1A), participants were asked to remember the locations of three red target circles, and no yellow distractor circles were presented at any stage. In the Encoding Distraction (ED) condition (Fig. 1B), two yellow distractor circles were shown together with the three red target circles. One of the yellow distractor circles was always in a position adjacent to a target position. In the Delay Distraction (DD) condition (Fig. 1C), two yellow distractor circles were shown during the WM delay period. One of the yellow distractor circles was always in a position adjacent to a target position. In all of these conditions, the to-be-remembered items were limited to three (i.e., three red target circles), since it has been shown that this set size could effectively establish distractor resistance effects during both the encoding and maintenance phases of WM (indicating separate ED and DD mechanisms; McNab and Dolan 2014). In addition, sticking to a set size of three allowed us to avoid potential confounds of strategy because with set size varying, at some point, it becomes easier for participants to remember the number of empty spaces in the grid rather than the number of to-be-remembered targets.

For each condition, the trial started with a blue fixation presented for 1 s in the center of the screen. Then red target circles (and yellow circles in the ED condition) were displayed for 1 s followed by a delay period of 3 s. During this delay period, a circular grid of 16 squares was shown, and two yellow distractor circles were presented in the DD condition, 0.5 s after the red target circles had disappeared. Each trial ended with a question mark presented either in or adjacent to one of the target positions for 2 s, 3 s after the target stimuli had disappeared. Participants were asked to give a yes/no response to indicate whether the probe was in a position that had been occupied by a red target circle. The circular grid remained on the screen throughout each trial. Targets were positioned such that no more than two targets were in adjacent positions. Half of the trials in each condition required a “yes” response, and in both the ED and DD conditions, half of the trials that required a “no” response had the probe presented in the position of a distractor.

To estimate each individual’s WM performance in each condition, WM performance was estimated with the K value, using a standard formula (Cowan 2001; Vogel et al. 2005); $K = S(H - F)$, where K is WMC, S is the number of to-be-remembered target items (i.e., 3), H is the observed hit rate, and F is the false alarm rate. This formula essentially assumes that if an observer can hold in memory K items from an array of S items, then the probed item that changed should be one of the items being held in memory on K/S trials, leading to correct performance on K/S of the trials on which an item changed. Importantly, it uses the false alarm rate to correct for guessing performance, leading to a more precise estimation of WM performance. Consequently, the maximum K value is 3 for each condition, and for each participant we calculated three

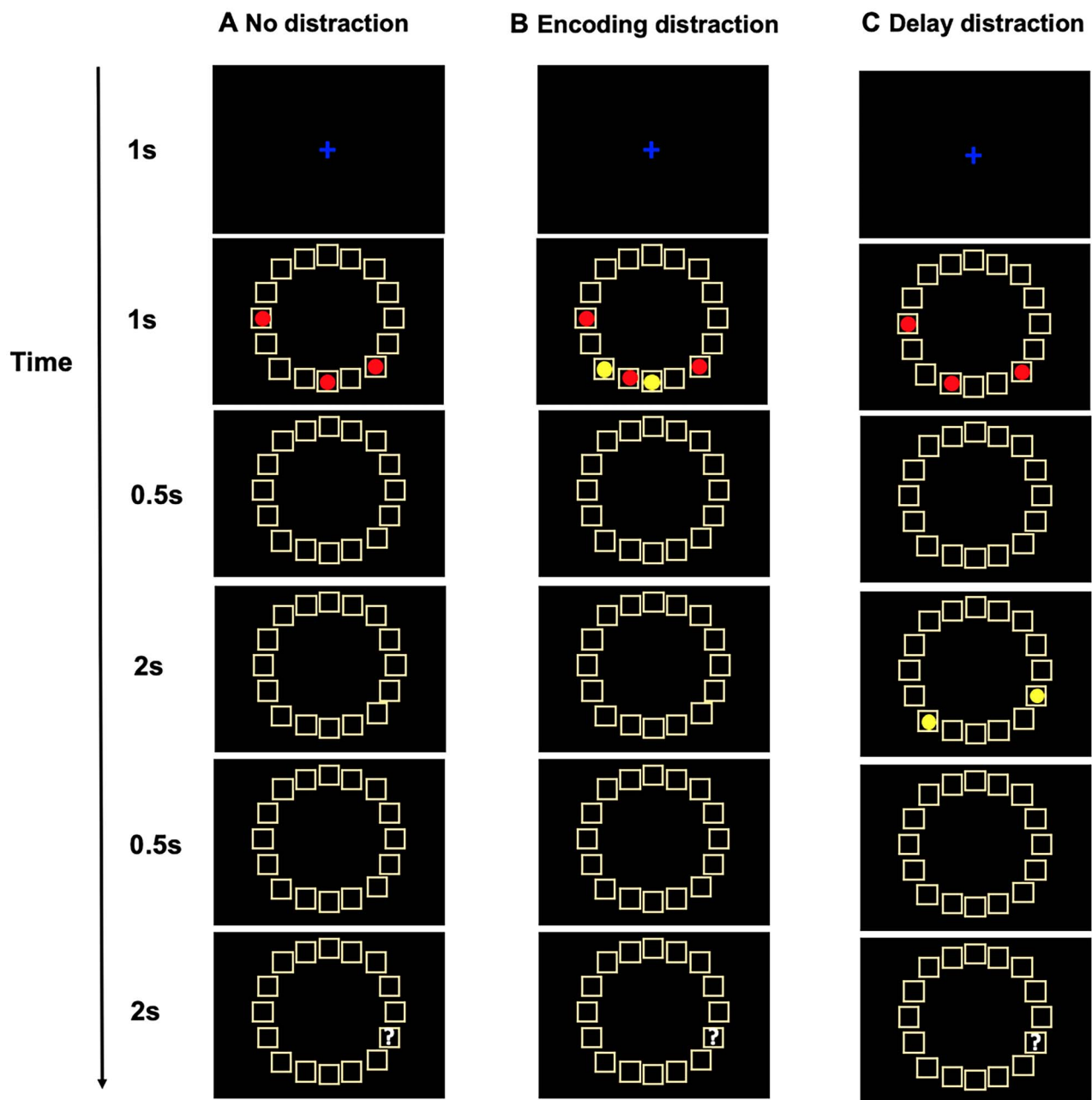


Figure 1. Task illustration of (A) no distraction (ND), (B) encoding distraction (ED), and (C) delay distraction (DD) trials. Participants were asked to maintain the locations of red targets; on encoding distractor trials, these targets were presented together with task-irrelevant yellow stimuli, while on delay distraction trials, the yellow distractors were presented after encoding, when the target information was no longer on the screen. Working memory (WM) performance was estimated with the K value for each condition, using a standard formula $K = \text{Number of to-be-remembered items} * (\text{Hit rate} - \text{False alarm rate})$ (Cowan 2001; Vogel et al. 2005). To assess each individual's ED and DD resistance abilities, we used regression analysis to estimate the residual in WM performance in the ED condition after accounting for WM performance in the DD condition (regression model: $ED = \alpha + \beta DD$), and the residual in WM performance in the DD condition after accounting for WM performance in the ED condition (regression model: $DD = \alpha + \beta ED$). The estimated ED and DD residuals were used as main explanatory variables after accounting for shared variance between them, since these scores represent unique variance associated with ignoring that type of distraction.

K values: one for the ND condition, one for the ED condition, and another for the DD condition.

To confirm our previous findings that ED and DD make a unique contribution to WM, we performed a regression analysis. In this regression, WM performance in the ED and DD conditions was used to predict WM in the ND condition. We used the regression model $ND = \alpha + \beta_1 ED + \beta_2 DD$, where ND, ED, and DD represent K values

for the ND, ED, and DD conditions respectively, α is the intercept and β_1 and β_2 are the regression coefficients. As K values for both ED and DD conditions were included in the model, we could examine the unique contribution of each to WM measure of ND performance. Following this approach, we used regression analysis to estimate ED and DD resistance ability for each participant ($N = 135$; also see Ashton et al. 2020; McNab and Dolan 2014). For

ED resistance ability, we used the residual in WM performance in the ED condition after accounting for WM performance in the DD condition, using the regression model $ED = \alpha + \beta DD$, where K values for the ED condition were taken as the dependent variable while K values for the DD condition were the predictor. Similarly, for DD resistance ability we used the residual in WM performance in the DD condition after accounting for WM performance in the ED condition using the regression model $DD = \alpha + \beta ED$, where K values for the DD condition were the dependent variable while K values for the ED condition were used as a predictor. In these regression models, the residuals for both ED and DD conditions were estimated for each individual by calculating the differences between the observed K value and the predicted K value for each condition (i.e., $\text{Residual} = \text{Observed } K \text{ value} - \text{Predicted } K \text{ value}$), since the residual for each observed K value for each condition indicates the variance that is left over in the data; that is, the variability that could not be explained by the other type of WM distraction. In this way, our measures of ED and DD resistance ability represent the unique variance associated with ignoring that type of distraction, controlling for shared variance associated with WM for relevant stimuli and instructions to ignore yellow circle distractors.

Neuroimaging Data Acquisition

Structural and functional data were acquired using a 3T GE HDx Excite magnetic resonance imaging (MRI) scanner utilizing an eight-channel phased array head coil at the York Neuroimaging Centre, University of York. Structural MRI acquisition in all participants was based on a T1-weighted 3D fast spoiled gradient echo sequence (repetition time (TR)=7.8 s, echo time (TE)=minimum full, flip angle=20°, matrix size=256 × 256, 176 slices, voxel size=1.13 mm × 1.13 mm × 1 mm).

A 9-min resting-state fMRI scan was used, recorded using single-shot 2D gradient-echo-planar imaging (TR=3 s, TE=minimum full, flip angle=90°, matrix size=64 × 64, 60 slices, voxel size=3 mm × 3 mm × 3 mm, 180 volumes). During resting-state scanning, participants were instructed to focus on a fixation cross with their eyes open and to keep as still as possible, without thinking about anything in particular. The resting-state data were collected first, followed by the collection of behavioral task data outside the scanner, so that measures of intrinsic connectivity could not be influenced by task performance.

Neuroimaging Data Preprocessing

Preprocessing was performed using the CONN-fMRI functional connectivity toolbox, Version 18a (<http://www.nitrc.org/projects/conn>; Whitfield-Gabrieli and Nieto-Castanon 2012), based on Statistical Parametric Mapping 12 (<http://www.fil.ion.ucl.ac.uk/spm/>). Participants' motion estimation and correction were then carried out through functional realignment, and unwarping and potential outlier scans were identified using the Artifact

Detection Tool (ART) toolbox (https://www.nitrc.org/projects/artifact_detect). Structural images were segmented into gray matter, white matter, and cerebrospinal fluid tissues and normalized to the Montréal Neurological Institute (MNI) space with the unified segmentation and normalization procedure (Ashburner and Friston 2005). Functional volumes were slice-time (bottom-up, interleaved) and motion-corrected, skull-stripped, and coregistered to the high-resolution structural image, spatially normalized to the MNI space using the unified-segmentation algorithm, smoothed with an 8 mm FWHM Gaussian kernel.

Preprocessing steps automatically create three first-level covariates: a *realignment* covariate containing the six rigid-body parameters characterizing the estimated subject motion for each participant, a *scrubbing* covariate containing the potential outliers scans for each participant (all outlier volumes were identified through the artifact detection algorithm included in CONN, with conservative settings: Scans for each participant were flagged as outliers based on scan-by-scan change in global signal above $z=3$, subject motion threshold above 0.5 mm, differential motion and composite motion exceeding 95% percentile in the normative sample), and a covariate containing quality assurance (QA) parameters (i.e., the global signal change from one scan to another and the framewise displacement, a measure of how much the participant moved from one scan to another) for each participant. Realignment parameters, potential outlier scans, signal from white matter and cerebrospinal fluid masks, and effect of rest (i.e., an automatically estimated trend representing potential ramping effects in the BOLD time series at the beginning of the sessions) were then included as nuisance parameters into the model in the denoising step of the CONN toolbox. Using the implemented anatomical CompCor approach components (Behzadi et al. 2007), all of these effects were removed within a general linear regression model to increase the signal-to-noise ratio in functional images (Chai et al. 2012). Functional images were then band-pass filtered (0.008–0.09 Hz) to constrain analyses to low-frequency fluctuations. A linear detrending term was also applied, eliminating the need for global signal normalization (Murphy et al. 2009; Chai et al. 2012). Global signal regression was not performed because CompCor can account for subject movement effects and other sources of noise in the BOLD signal (Behzadi et al. 2007; Muschelli et al. 2014).

ROI Selection and Resting-State fMRI Analysis

Our seeds were derived from two large-scale network maps (similar to Beaty et al. 2021; Evans et al. 2020; Lee et al. 2021), allowing us to assess how variation in intrinsic connectivity from whole distributed networks relates to WM performance. These maps were defined by Yeo et al. (2011) using a seven-network parcellation of 1000 resting-state scans: We examined 1) DMN, which is implicated in the heteromodal aspects of memory

representations (Spreng et al. 2009; Andrews-Hanna et al. 2010; Margulies et al. 2016), and 2) FPN, which plays a central role in cognitive control (Cole et al. 2013). While we had specific hypotheses about coupling and decoupling of these networks from visual cortex, given we examined performance on a visual-spatial task, we did not constrain our analysis to visual cortex, since there might also be decoupling from other primary systems suited to encoding locations in space, such as motor cortex (e.g., Postle et al. 2000), as well as decoupling from external visual attention regions (e.g., Yantis et al. 2002). These types of perceptual decoupling might relate to better distraction resistance during the maintenance phase, since they could also reduce distraction from the external environment to benefit active maintenance in WM. In addition, it has been shown that internet-work connectivity within DMN is related to better WM performance (Hampson et al. 2006; Vatansever, Manktelow, et al. 2017): For this reason, our network seed regions were not masked during the analysis—it remained possible to observe within-network connectivity changes in our whole-network seed-to-voxel analysis.

Our analysis obtained whole-brain maps that described the strength of functional connectivity of each voxel in the brain with the seed network, to explore associations between task performance and the intrinsic connectivity of DMN and FPN. In a first-level analysis, we extracted the residual BOLD time series (i.e., the BOLD time series after preprocessing and denoising steps) from selected ROIs in each subject, and calculated the mean across the voxels within each network seed for each time point. To obtain the seed-based connectivity map for each subject, the Pearson's correlation coefficient between the time series of each voxel in the brain and the mean time series of the seed ROI was calculated by applying bivariate correlation and hemodynamic response function (hrf) weighting, which offers additional protection against transient effects in the BOLD signal at the beginning of scanning. The resulting correlation was entered into the connectivity map at the location of each voxel. This was repeated for all of the voxels in the brain (i.e., including the voxel within the seed region), resulting in a whole-brain connectivity map. Then correlation coefficients were converted to normally distributed scores using Fisher's transform for second-level GLM analysis. For this second-level analysis, the explanatory variables (EVs) were entered into a GLM, including the ability to resist encoding distractors (i.e., the residual WM performance in the ED condition after accounting for performance in the DD condition) and the ability to resist distractors presented during the delay (i.e., the residual WM performance in the DD condition after accounting for performance in the ED condition). In this way, the intrinsic connectivity patterns relating to each aspect of distractor resistance ability accounted for performance in the other condition.

We used two-sided tests to determine significant clusters, which allowed us to simultaneously examine patterns of both stronger and weaker functional connectivity. We defined the following contrasts of interest for each seed to examine the main effects of each experimental condition, and the contrasts between conditions ("ED > DD resistance ability", and "DD > ED resistance ability"). Group-level analyses in CONN were thresholded at a "height" or "cluster-defining" threshold of $P < 0.005$ (two-sided tests) to define a series of nonoverlapping clusters, and among this resulting suprathreshold map, only clusters with a cluster-size FWE corrected $P < 0.05$ were identified. These group-level differences were examined using a GLM. We also applied the Bonferroni correction to account for the fact that we included two models (FPN and DMN). Consequently, the cluster-size FWE corrected P -value accepted as significant was < 0.025 . All figures were created using BrainNet Viewer (<http://www.nitrc.org/projects/bnv/>; Xia et al. 2013).

Prior to data analysis, all behavioral variables were z -transformed and outliers more than 2.5 SDs above or below the mean were identified. These outlying values were imputed with the cutoff value (i.e., ± 2.5 SDs above or below the mean).

Data and Code Availability Statement

Neuroimaging data at the group-level statistical t maps are openly available in Neurovault at <https://neurovault.org/collections/9355/>. The conditions of our ethical approval do not permit public archiving of the raw data because participants did not provide sufficient consent. Researchers who wish to access the data should contact the Research Ethics and Governance Committee of the York Neuroimaging Centre, University of York, or the corresponding authors. Data will be released to researchers when this is possible under the terms of the GDPR (General Data Protection Regulation).

Results

Behavioral Results

Values for WM performance for each of the conditions and zero-order correlations are shown in Table 1. Performance declined with the inclusion of distractors, and a one-way ANOVA revealed a significant effect of condition, $F(2,262) = 6.02$, $P = 0.003$. Post hoc paired t -tests revealed a statistically significant difference between the K values from the ND and DD conditions, $t(131) = 3.62$, uncorrected $P < 0.001$, but not between the ND and ED conditions, $t(131) = 1.68$, uncorrected $P = 0.10$, or between the two distraction conditions, $t(131) = 1.72$, uncorrected $P = 0.09$. The small difference between these conditions in our study is consistent with a previous study which used the same paradigm (McNab and Dolan 2014). Though the absolute difference between conditions is small, we focus here on individual differences across conditions.

Table 1. Mean working memory performance (K) for each condition and the results of Pearson correlations between K values for each condition.

	No distraction	Encoding distraction	Delay distraction
Mean working memory performance (K value \pm SD)	2.72 \pm 0.29	2.67 \pm 0.34	2.62 \pm 0.36
Results of the Pearson correlation between K values for each condition (R)			
No distraction		0.50***	0.51***
Encoding distraction			0.43***

*** $P < 0.001$.**Table 2.** Results for regression model with ED and DD as predictors.

Predictor	Adjusted R^2	Standardized beta	Coefficients standard error	P value	95% CI for B		Partial correlation
					Lower bound	Upper bound	
ED	0.34	0.34	0.07	<0.001	0.16	0.42	0.36***
DD		0.36	0.06	<0.001	0.16	0.42	0.37***

Note: CI = Confidence interval. *** $P < 0.001$. Note: The results of partial correlations show the strength and direction of the correlation of each predictor (i.e., the K values for the ED or DD conditions) with the K values for the ND condition, while controlling for the effect of the other predictor variable.

In addition, these K values of ND, ED, and DD conditions positively correlated with each other (see Table 1).

Using the regression model: $ND = \alpha + \beta_1 ED + \beta_2 DD$, where ND, ED, and DD represent K values for the ND, ED, and DD conditions, respectively; α is the intercept; and β_1 and β_2 are the regression coefficients, we confirmed previous findings showing a unique contribution of ED and DD performance to WM in the absence of overt distraction (McNab and Dolan 2014; McNab et al. 2015). As shown by Table 2, ED and DD performance together significantly predicted WM (adjusted $R^2 = 0.34$, $F(2,129) = 34.93$, $P < 0.001$). Both K values for ED and DD conditions significantly and uniquely predicted WM, while controlling for performance in the other condition (ED: standardized $\beta = 0.34$, $P < 0.001$; DD: standardized $\beta = 0.36$, $P < 0.001$). Also, in line with our previous findings, these were positive associations, indicating that greater distractor resistance is associated with better WM performance. Contrary to our previous findings (McNab and Dolan 2014), a significant positive correlation was seen between K values for ED and DD conditions (partial correlation controlling for K values for the ND condition, $r = 0.24$, $P = 0.006$), reflecting shared variance between ED and DD resistance performance. Therefore, we used the estimated ED and DD residuals after accounting for WM performance in the other type of distraction condition as our main explanatory variables (i.e., obtained using the regression analyses described in the Behavioral Assessment); these variables represent unique variance associated with ignoring each type of distraction. The residuals in K values for the ED and DD conditions were positively correlated with K values for the ND condition (ED: $r = 0.31$, $P < 0.001$; DD: $r = 0.32$, $P < 0.001$; see Fig. 2A,B), suggesting unique contributions of these aspects of distractor resistance to WM performance.

Resting-State Functional Connectivity Results for the FPN Seed

We found that FPN connectivity was related to individual differences in DD resistance ability. Participants with weaker intrinsic connectivity at rest between FPN and visual areas, including precuneus and lateral occipital cortex, were less likely to be affected by distractors presented during the delay (cluster-size P-FWE value < 0.001 at height threshold $P < 0.005$ and cluster-size P-FWE value = 0.003 at height threshold $P < 0.001$; all of these cluster-size P-FWE values were the Bonferroni corrected for two seeds). These findings are shown in (Fig. 3A) and suggest a role for perceptual decoupling in allowing the FPN to be involved in maintenance of the contents of WM. Of those voxels within this cluster that fell within the large-scale networks defined by Yeo et al. (2011), 82% were within the visual network, 12% were within dorsal attention network, and 6% fell within DMN (see Fig. 3B). Meta-analytic decoding of this functional connectivity map using Neurosynth yielded terms associated with visual processing, such as “visual”, “objects”, and “navigation” (see Fig. 3C). Together, this pattern of results suggests that participants who showed better ability to ignore distractors during a WM delay period had greater decoupling of FPN from visual areas.

There were no significant associations between FPN connectivity and individual differences in ED resistance ability. This absence of effects during the encoding phase of WM might relate to the internal-external functional distinction of FPN subsystems (Dixon et al. 2018), as suggested by our supplementary analyses. Greater functional decoupling of DMN from the FPN subsystem associated with external cognition (and anticorrelated with the DMN) was associated with better ability to resist encoding distraction (see Supplementary Fig. 1 in Supplementary Materials). This greater separation between

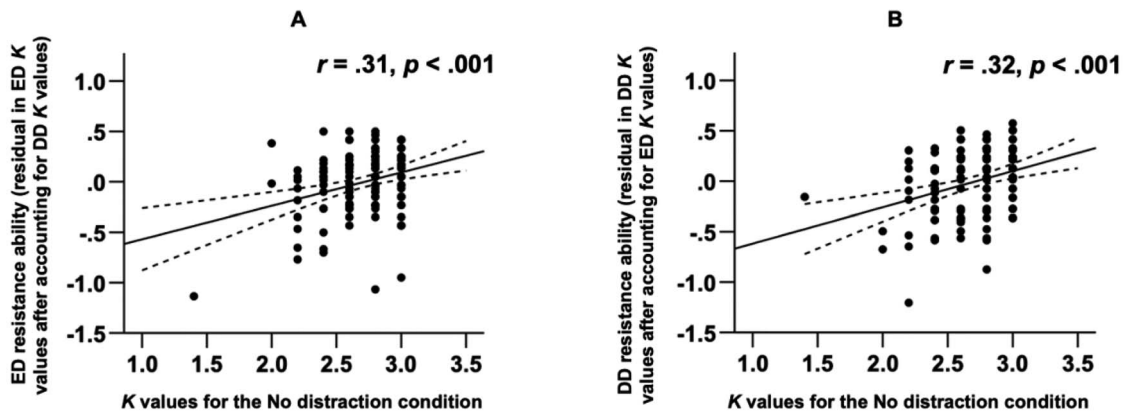


Figure 2. Positive associations between WM performance in the ND condition and (A) ED resistance ability (the residual in ED K values after accounting for DD K values), (B) DD resistance ability (the residual in DD K values after accounting for ED K values). The positive associations indicate that greater distractor resistance is associated with better WM performance. Each point indicates a single participant, with some data points superimposed. The error lines on the scatterplot indicate the 95% confidence estimates of the mean.

external FPN and DMN might allow DMN to better support internal representations of target information during the encoding phase. In addition, both this external control subnetwork and the FPN subnetwork linked to internal aspects of cognition (i.e., the regulation of introspective processes) exhibited greater functional decoupling from visual areas, including lateral occipital cortex and precuneus cortex, for individuals with better DD resistance ability (see [Supplementary Figs 1 and 2](#) in [Supplementary Materials](#)), resembling the decoupling pattern identified for our main FPN network seed. This converging evidence reveals the important functional role of perceptual decoupling of FPN in supporting better maintenance of target information in the face of irrelevant external information.

Results for the DMN Seed

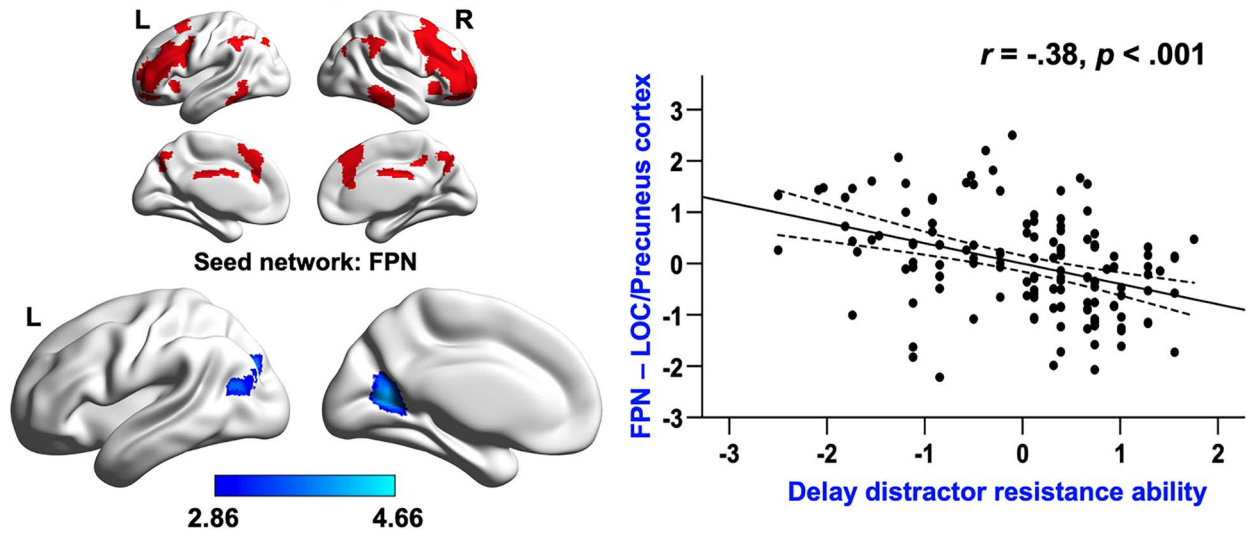
Main effects of distractor resistance ability

The intrinsic connectivity of DMN was associated with both encoding and delay distractor resistance ability in different ways. Participants with better ED resistance ability had stronger connectivity from DMN to retrosplenial cortex (see the left red column in [Fig. 4A](#); cluster-size P -FWE value < 0.001 at height threshold $P < 0.005$ and cluster-size P -FWE value $= 0.003$ at height threshold $P < 0.001$; all of these cluster-size P values were Bonferroni corrected for two seeds). Of those voxels within this identified cluster that fell within large-scale networks defined by [Yeo et al. \(2011\)](#), 69% were within DMN, and 31% were within the visual network (see the left panel of [Fig. 4B](#)). Meta-analytic decoding of this functional connectivity map using Neurosynth yielded terms associated with DMN, such as “episodic” and “autobiographical memory” (see [Fig. 4C](#)). In contrast, for individuals with better DD resistance ability, DMN showed weaker connectivity with lingual gyrus within primary visual cortex (see the blue panel in [Fig. 4A](#); cluster-size P -FWE value $= 0.038$ Bonferroni corrected for two seeds at height

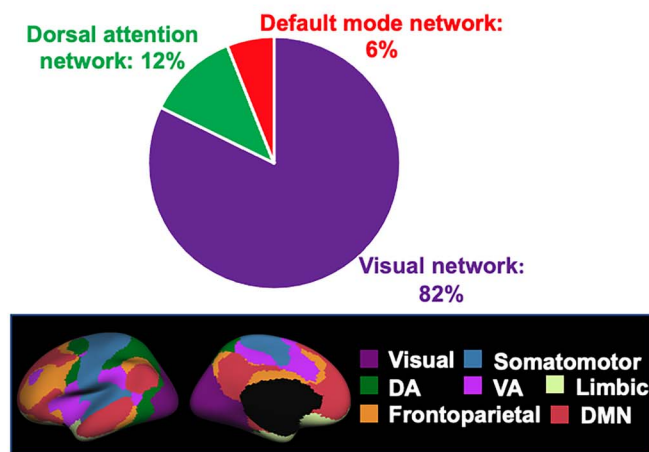
threshold $P < 0.005$; no significant cluster identified at height threshold $P < 0.001$ - The absence of visual decoupling of DMN at this more stringent threshold might reflect a Type II error since visual decoupling of FPN and DMN are similar at a lower cluster-forming threshold of $P < 0.005$). Of those voxels within this identified cluster that fell within large-scale networks defined by [Yeo et al. \(2011\)](#), 100% were within the visual network (see the right panel of [Fig. 4B](#)). Meta-analytic decoding of this functional connectivity map using Neurosynth yielded terms associated with visual processing, such as “visual” and “faces” (see [Fig. 4D](#)). In summary, participants who were able to better encode the locations of targets despite concurrently presented distractors had stronger connectivity of DMN to retrosplenial cortex associated with the representation of spatial location; furthermore, participants who were better able to ignore distractors during the maintenance phase had stronger decoupling of DMN from primary visual areas.

The results above revealed that FPN had weaker intrinsic connectivity with medial visual areas for individuals with better DD resistance ability, while stronger connectivity of DMN with medial visual areas was associated with better ED resistance ability. In order to establish if there were opposing yet overlapping patterns of intrinsic connectivity in medial visual cortex related to resistance to distractors presented during the encoding and delay periods, we overlapped these two maps. Both effects were significant in medial visual areas, including precuneus and supracalcarine cortex (see [Fig. 5](#)). Of the voxels within this overlap map, 82% were within the visual network, and 18% were within DMN (see the pie chart in [Fig. 5](#)). Stronger coupling of DMN to medial visual cortex is associated with good WM performance when targets are presented concurrently with distractors, while functional decoupling of FPN from the same visual region is associated with the ability to resist distractors presented in the delay period.

A Functional connectivity seeding from FPN



B Overlap with Yeo et al.'s 7 networks



C Neurosynth decoding



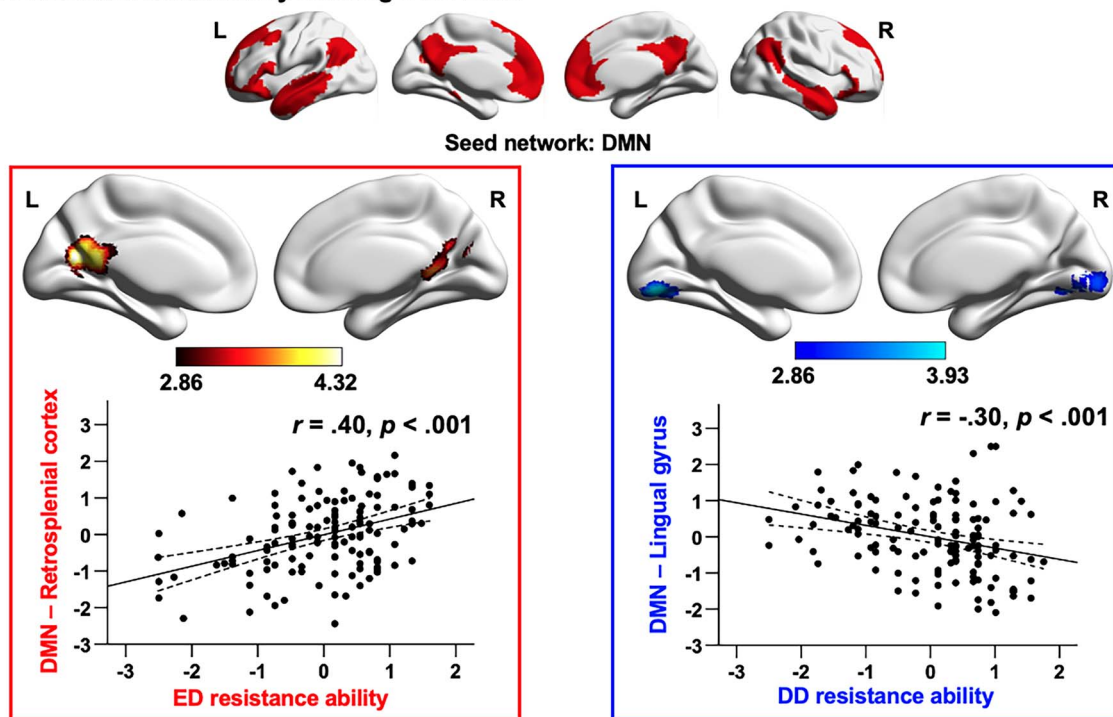
Figure 3. Functional connectivity of FPN linked to DD resistance ability. (A) Regions in blue showed weaker connectivity with the FPN seed for participants with better DD resistance ability. All maps are cluster-corrected using a height threshold of $P < 0.005$ (cluster-size P -FWE < 0.05). The scatterplot shows the relationship between intrinsic connectivity with FPN (beta values) in the identified cluster and DD resistance scores. The error lines on the scatterplot indicate the 95% confidence estimates of the mean. Each point describes each participant. (B) The pie chart illustrates the percentage of voxels in the identified cluster that fell within the large-scale networks defined by Yeo et al.'s (2011) 7-network parcellation, disregarding voxels that did not fall within any of the Yeo networks. (C) Meta-analytic decoding of this functional connectivity map using the Neurosynth database revealed a number of terms associated with visual processing, such as “visual”, “objects”, and “navigation”. DA = Dorsal attention; VA = Ventral attention; LOC = Lateral occipital cortex; L = Left hemisphere; R = Right hemisphere.

Direct contrast between varieties of distractor resistance

Stronger intrinsic connectivity between DMN and regions of retrosplenial cortex, precuneus, posterior cingulate cortex, and lingual gyrus was associated with better resistance to encoding distraction relative to delay distraction (see Fig. 6A; cluster-size P -FWE value < 0.001 at both height threshold of $P < 0.005$ and $P < 0.001$; all of these cluster-size P values were Bonferroni corrected for two seeds). Of those voxels within this identified cluster that fell within large-scale networks defined by Yeo et al. (2011), 60% were within DMN and 40% were within the visual network (see Fig. 6B). Meta-analytic

decoding of this functional connectivity map using Neurosynth yielded terms associated with DMN, such as “episodic memory” and “autobiographical memory”, and also terms associated with spatial processing, such as “navigation” (see Fig. 6C). This pattern of results suggests that participants who were better able to ignore distractors presented simultaneously with targets, compared with distractors presented in a delay period, had stronger connectivity of DMN to both DMN and visual regions. There was no stronger connectivity relating to better DD resistance ability compared with ED resistance ability. We also did not find any significant effects in the FPN

A Functional connectivity seeding from DMN



B Overlap with Yeo et al.'s 7 networks



C Neurosynth decoding of DMN connectivity linked to ED resistance ability



D Neurosynth decoding of DMN connectivity linked to DD resistance ability

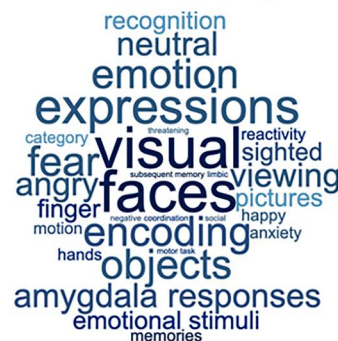


Figure 4. Functional connectivity of DMN linked to distractor resistance ability at encoding and delay. (A) The regions in red showed stronger connectivity with the DMN seed in participants with better distractor resistance during encoding, while the regions in blue showed weaker connectivity with the DMN seed in individuals with better distractor resistance during the delay. All maps are cluster-corrected using a height threshold of $P < 0.005$ (cluster-size $P\text{-FWE} < 0.05$). The scatterplots present the relationship between intrinsic connectivity with DMN (beta values) in the identified clusters and behavioral performance (i.e., encoding and delay distractor resistance ability). The error lines on the scatterplots indicate the 95% confidence estimates of the mean. Each point describes each participant. (B) The pie charts illustrate the percentage of voxels in the identified clusters that fell within the large-scale networks defined by Yeo et al.'s 7-network parcellation (2011), disregarding voxels that did not fall within any of the Yeo networks. (C, D) Meta-analytic decoding of these functional connectivity maps using the Neurosynth database revealed a number of terms associated related with the DMN, such as “episodic” and “autobiographical memory”, for the connectivity map linked to ED resistance ability, and a number of terms related to visual processing, such as “visual” and “faces”, for the connectivity map linked to DD resistance ability. L = Left hemisphere; R = Right hemisphere.

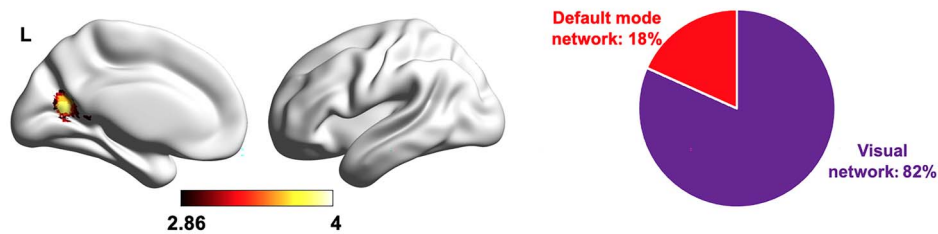


Figure 5. Overlay of results in medial visual cortex. The positive DMN connectivity effect related to ED resistance ability was overlapped with the negative FPN connectivity effect related to DD resistance ability in medial visual cortex, by identifying common voxels with t values >2.86 (i.e., t threshold at the height threshold of $P < 0.005$) in both connectivity maps. The figure highlights voxels present in both clusters, while the pie chart illustrates the percentage of voxels in both clusters that fell within the large-scale networks defined by Yeo et al.'s 7-network parcellation (2011), disregarding voxels that did not fall within any of the Yeo networks. L = Left hemisphere.

connectivity patterns in this direct contrast of these two conditions.

Discussion

The ability to resist distracting information is a key determinant of WM, helping individuals encode and maintain goal-relevant information in mind (Vogel et al. 2005; McNab and Dolan 2014). Since this capacity involves both encoding information in the environment and maintaining mental contents in the face of distracting and task-irrelevant sensory changes, individual differences in WM capacity may relate to the diverse ways in which regions of heteromodal cortex can couple with and decouple from perceptual systems. Here, we identify the patterns of intrinsic connectivity that are associated with individual differences in these distinct components of WM. Using a visuospatial WM task, we assessed the capacity of participants to ignore distractors presented at encoding (Encoding Distraction; ED) or in a delay period (Delay Distraction; DD). Individual differences in these two aspects of distractor resistance ability related to the functional connectivity of two heteromodal networks—FPN, which plays a central role in cognitive control (Cole et al. 2013), and DMN, which is implicated in stimulus-independent thought and memory-guided decision-making (e.g., Konishi et al. 2015; Murphy, Wang, et al. 2019). Individuals with better ED resistance ability had stronger connectivity of DMN with retrosplenial cortex and medial visual areas. In contrast, for individuals with better DD resistance ability, FPN had stronger disconnection from lateral occipital cortex and overlapping medial visual areas, while DMN showed stronger decoupling from primary visual areas. Stronger intrinsic connectivity of DMN with medial visual areas and retrosplenial cortex might support the ability to separate target and distractor locations during encoding, while greater decoupling of both FPN and DMN from visual processes might support the maintenance of target locations in the face of visual distractors presented during a delay period.

Our study builds on existing evidence that both the FPN and DMN are implicated in WM (Gazzaley and D'Esposito 2007; McNab and Klingberg 2008; Duncan 2010; Gazzaley and Nobre 2012; Konishi et al. 2015;

Murphy et al. 2018). Control processes within FPN support both the encoding and maintenance of task-relevant information (Zanto et al. 2011; Gazzaley and Nobre 2012), especially when distractors can interfere with target representation (Chao and Knight 1998; McNab and Klingberg 2008; Konstantinou et al. 2014). Additionally, DMN is involved in the internal representation of self-generated states (Mason et al. 2007; Christoff et al. 2009; Konu et al. 2021) and task-relevant information (Crittenden et al. 2015; Vatansever, Menon, et al. 2017; Murphy et al. 2018; Wang et al. 2021). Our results complement these studies by highlighting the important role that these systems play in different features of WM through their coupling and decoupling with regions involved in perceptual processing.

We established that stronger connectivity between DMN and medial parietal and visual areas, including retrosplenial cortex, was associated with an enhanced ability to resist distracting information concurrently presented with targets, indicating a role in efficient encoding of information into WM. Meta-analytic evidence (see Fig. 4) supports the view that medial parietal cortex is implicated in aspects of cognition supported by internal memory representations (for a review, see Leech and Smallwood 2019); retrosplenial cortex, in particular, plays a role in spatial memory and navigation (Maguire 2001; Epstein 2008; Czajkowski et al. 2014; Ekstrom et al. 2017), with stronger connectivity between this site and DMN associated with better spatial performance (Sulpizio et al. 2016). This region is also implicated in the retrieval of episodic and autobiographical memory (Svoboda et al. 2006; Kaboodvand et al. 2018) and is linked to detailed focus during self-relevant processing (Murphy, Poerio, et al. 2019). Retrosplenial cortex is proximal to both medial visual regions and areas of medial parietal cortex associated with internally oriented cognition: Our cluster extended across both of these regions, perhaps reflecting the requirements of the task to transform visual codes into spatial representations. Given these findings, stronger connectivity of DMN with retrosplenial cortex might allow participants to better distinguish the spatial locations of targets from nontargets, thus aiding more efficient or more selective encoding of target information in the face of concurrent distractors placed in nearby locations.

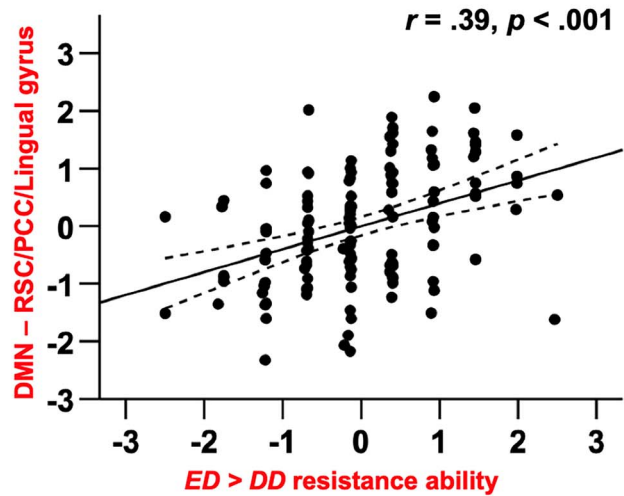
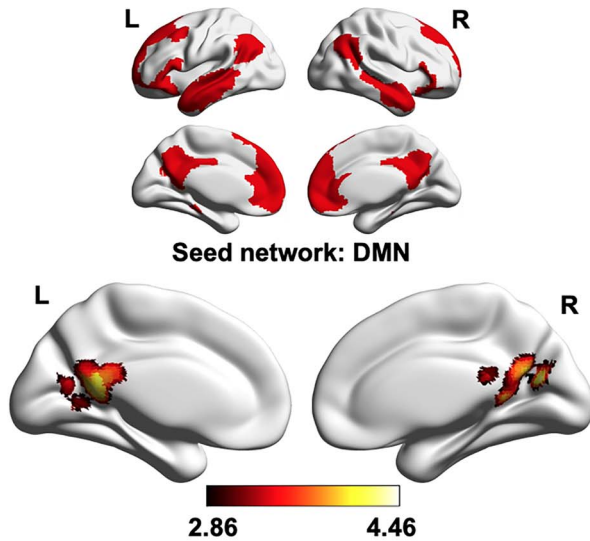
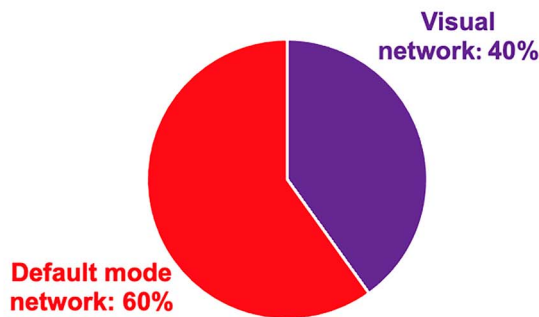
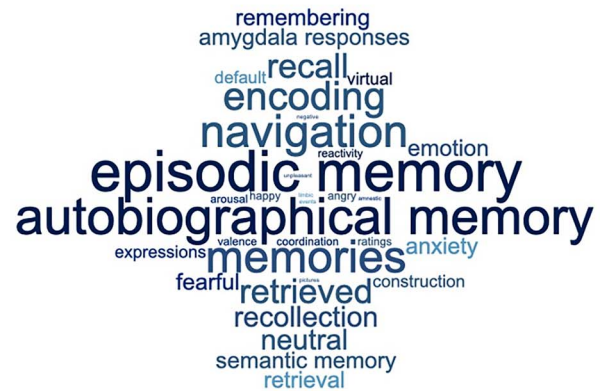
A ED > DD resistance ability seeding from DMN**B Overlap with Yeo et al.'s 7 networks****C Neurosynth decoding**

Figure 6. Results of direct contrast between varieties of distractor resistance. (A) Regions of higher connectivity with the DMN seed were associated with better resistance to encoding distraction relative to delay distraction. All maps are cluster-corrected using a height threshold of $P < 0.005$ (cluster-size P -FWE < 0.05). The scatterplot shows the relationship between average DMN connectivity (beta values) in the identified cluster and behavioral difference scores relating to ED > DD resistance ability. The error lines on the scatterplot indicate the 95% confidence estimates of the mean. Each point describes each participant. (B) The pie chart illustrates the percentage of voxels in the identified cluster that fell within the large-scale networks defined by Yeo et al.'s 7-network parcellation (2011), disregarding voxels that did not fall within any of the Yeo networks. (C) Meta-analytic decoding of this functional connectivity map using the Neurosynth database revealed a number of terms associated with DMN, such as “episodic memory” and “autobiographical memory”, and also terms related to spatial processing, such as “navigation”. RSC=Retrosplenial cortex; PCC=Posterior cingulate cortex; L=Left hemisphere; R=Right hemisphere.

The capacity to ignore distractors presented during a delay, rather than concurrently with targets, was associated with a different pattern of connectivity (i.e., perceptual decoupling), supporting a long-standing psychological hypothesis that the capacity to decouple attention from perception helps to maintain internal representations (Smallwood 2013). Functional decoupling of both FPN and DMN from visual cortex was related to better distractor resistance during target maintenance, yet these effects were localized to different visual areas. FPN showed decoupling from LOC alongside medial visual regions, while DMN was decoupled from primary visual cortex. Primary visual cortex acts as a perceptual gate allowing visual inputs to be perceived and forwarded to higher regions (see Fig. 4D; Tong 2003; Kok and de Lange

2014; Zhang et al. 2021). During target maintenance, decoupling of DMN from primary visual regions might reduce interference from visual stimuli in the immediate environment (Chadick and Gazzaley 2011). In contrast, lateral and medial visual cortex might be essential for internally directed aspects of mental states, given that memory retrieval involves access to encoded visual features (e.g., Fletcher et al. 1996; Rubin and Greenberg 1998; Greenberg and Rubin 2003); stronger activation of these areas was associated with better autobiographical memory retrieval in a recent study (Zhang et al. 2020). Consequently, decoupling of FPN from medial and lateral visual areas might reflect reduced higher-level processing of distracting visual inputs. FPN plays a key role in maintaining relevant information in the face of delay

distraction (Sakai et al. 2002; Jha et al. 2004; Feredoes et al. 2011); moreover, Clapp et al. (2010) found decoupling of control sites from sensory cortex was linked to less distraction during WM maintenance, in line with our findings. The top-down regulation of perceptual regions by control sites is thought to support the encoding of visual information (Gazzaley and D'Esposito 2007; Gazzaley and Nobre 2012)—participants with stronger coupling between FPN and medial and lateral visual cortex might conceivably have more difficulty avoiding visual encoding during periods when presented items are task-irrelevant.

These findings provide converging evidence about the important role that perceptual decoupling of heteromodal cortex plays in supporting the maintenance of goal-relevant information in the face of distracting information in the environment. More generally, our study is important for understanding why states of self-generated thought detract from the efficient processing of external information—sensory decoupling of regions of heteromodal cortex may help limit distractors in working memory. Viewed from this perspective, self-generated thought may lead to poor performance on external tasks because the integrity of this state depends upon reducing the influence of perceptual inputs (Smallwood 2013). Our results also demonstrate that opposing yet overlapping patterns of connectivity are associated with different processes important for visual WM: visual coupling is associated with better encoding, yet visual decoupling is associated with better maintenance, in line with the distinct contributions of encoding and delay distractor resistance in cognitive studies (McNab and Dolan 2014). Going beyond WM performance, recent studies have shown that functional connectivity of DMN regions to visual cortex can support visually mediated tasks, while visual decoupling of DMN is important for internally oriented cognition (Zhang et al. 2019, 2020). The different phases of the WM task we examined are similarly biased toward external cognition (for visual encoding) and internal cognition (maintenance through the delay period). The balance of functional coupling and decoupling between heteromodal and visual cortex might therefore influence the extent to which cognition supports fine-grained visual distinctions in the external world (e.g., between target and distractor locations) as opposed to the veridical maintenance of information in mind, while ignoring distracting perceptual events. More generally, our study provides important support for contemporary accounts of the way in which heteromodal cortex contributes across multiple cognitive domains through interactions with other brain regions (Smallwood et al. 2021).

Although our study clearly establishes that coupling and decoupling of heteromodal cortex are differentially important during encoding and maintenance of information in WM, it nevertheless leaves open several important questions. 1) Our study is unable to pinpoint whether the effects are directly related to distractor resistance or instead reflect indirect effects on WM capacity. For exam-

ple, better encoding distractor performance in participants with stronger visual coupling might be a result of more selective encoding of task-relevant information or instead could reflect stronger or more detailed encoding. Similarly, visual decoupling effects might be associated with better maintenance of target information or more successful retention of spatial information distinguishing target and nontarget locations. Nevertheless, our supplementary analysis highlights a general contribution of these patterns of perceptual coupling and decoupling to encoding and maintenance of target information, since they were also correlated with WM without distraction (see [Supplementary Fig. 3 in Supplementary Materials](#)). 2) This investigation used a constant WM load and highly predictable presentation of distractors, and consequently it does not establish whether these coupling and decoupling connectivity patterns are modulated by these factors. 3) While our study examines how individual differences in intrinsic connectivity relate to different features of WM, it cannot reveal how connectivity dynamically changes during task performance, between encoding, delay, and decision phases. We might expect participants with the strongest task performance to selectively couple heteromodal DMN and FPN networks to visual cortex during encoding and then decouple these networks during the delay period. A task-based fMRI study of the same paradigm could test this hypothesis. 4) Moreover, our resting-state fMRI data reflect spontaneous fluctuations in blood oxygenation level-dependent (BOLD) signals, rather than a task-induced state that is directly related to the processing of stimuli or online memory function. Therefore, the link between heteromodal-to-visual intrinsic connectivity and individual differences in distraction resistance ability reflects a neurocognitive trait, not a state. 5) Finally, resistance to irrelevant items during WM encoding has been linked to the basal ganglia (McNab and Klingberg 2008); this subcortical effect was not identified here.

In conclusion, we found that 1) the intrinsic connectivity of heteromodal systems (both DMN and FPN) was related to visuospatial WM performance; 2) that different patterns of connectivity were linked to individual differences during encoding and maintenance phases of the task; and 3) that functional coupling and decoupling of visual cortex was associated with these distinct stages. Perceptual coupling was associated with better distractor resistance during encoding, while perceptual decoupling was associated with better distractor resistance during the maintenance of internal target representations.

Supplementary Material

[Supplementary material](#) can be found at *Cerebral Cortex* online.

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Notes

Conflict of Interest: The authors have declared that no competing interests exist.

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