

RESEARCH ARTICLE

Neural activity during working memory encoding, maintenance, and retrieval: A network-based model and meta-analysis

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Abstract

It remains unclear whether and to what extent working memory (WM) temporal sub-processes (i.e., encoding, maintenance, and retrieval) involve shared or distinct intrinsic networks. To address this issue, I constructed a model of intrinsic network contributions to different WM phases and then evaluated the validity of the model by performing a quantitative meta-analysis of relevant functional neuroimaging data. The model suggests that the transition from the encoding to maintenance and to retrieval stages involves progressively decreasing involvement of the dorsal attention network (DAN), but progressively increasing involvement of the frontoparietal control network (FPCN). Separate meta-analysis of each phase effect and direct comparisons between them yielded results that were largely consistent with the model. This evidence included between-phase double dissociations that were consistent with the model, such as encoding > maintenance contrast showing some DAN, but no FPCN, regions, and maintenance > encoding contrast showing the reverse, that is, some FPCN, but no DAN, regions. Two closely juxtaposed regions that are members of the DAN and FPCN, such as inferior frontal junction versus caudal prefrontal cortex and superior versus inferior intraparietal sulcus, showed a high degree of functional differentiation. Although all regions identified in the present study were already identified in previous WM studies, this study uniquely enhances our understating of their roles by clarifying their network membership and specific associations with different WM phases.

KEYWORDS

encoding, fMRI, maintenance, meta-analysis, retrieval, working memory

1 | INTRODUCTION

1.1 | The aim of the study

Working memory (WM), an ability to hold and manipulate information “in the mind,” is a fundamental component of many everyday cognitive activities, such as reading comprehension, learning, problem solving, and planning. An important goal of WM cognitive neuroscience is to identify the neural mechanisms underlying its encoding, maintenance, and retrieval processes. To this end, many functional neuroimaging

studies employ various “delayed-response” paradigms that can dissociate the WM stages in time, such as the Sternberg Item Recognition Task, which consists of an encoding phase, during which subjects memorize a set of items; a maintenance phase, during which the information is held “online”; and a retrieval phase, during which subjects respond to a probe by indicating whether or not it was a member of the memorized set. While these studies expanded our understanding of the neural bases of WM temporal subprocesses, they also produced many between-study discrepancies and even direct contradictions. For

example, while many studies indicated that maintenance involved the prefrontal cortex (PFC), specific prefrontal sites showing this effect varied widely across studies (Cairo, Liddle, Woodward, & Ngan, 2004; Habeck et al., 2005; Manoach, Greve, Lindgren, & Dale, 2003; Passaro et al., 2013; Rypma & D'Esposito, 2000) and some even found no specific evidence of PFC involvement (Beatty et al., 2015; Majerus, Salmon, & Attout, 2013; Murty et al., 2011). While these diverse results per se are not necessarily surprising, given the many different stimuli types, procedures, and analytic methods employed, they make it difficult to draw general conclusions as to which brain regions reliably contribute to different WM phases.

Several studies performed quantitative meta-analyses of WM-neuroimaging data to identify significant concordance across individual studies. These studies typically focused exclusively on "n-back" tasks (Owen, McMillan, Laird, & Bullmore, 2005; Wang et al., 2019; Yapple & Arsalidou, 2018), which do not permit the separation of the different temporal phases, or collapsed analyses across data regarding n-back and other delayed-response tasks (Hill, Laird, & Robinson, 2014; Rottschy et al., 2011; Wager & Smith, 2003). Although a recent study (Daniel, Katz, & Robinson, 2016) focused exclusively on a delayed-response paradigm, namely, delayed match to sample, it did not perform any specific analysis relevant to the separation of different phase effects. In this regard, the present study aimed to provide the first meta-analysis identifying which specific brain regions are recruited during different WM phases. To formulate hypotheses for the meta-analysis and interpret the results, the present study also constructed a neurocognitive model of WM temporal subprocesses, as described in more detail below. Thus, this study strives to go beyond a generic purpose of integrating results across studies and potentially also contribute to neurocognitive theorizing of WM.

1.2 | An overview of the meta-analysis

A most fundamental aspect of all meta-analysis designs is determining which studies are included in and excluded from the analysis. Candidate studies for meta-analysis necessarily used WM tasks that separated three phase-epochs in time, but only a minority actually reported the activation effects of all three phases, whereas a majority reported only one- or two-phase effects (e.g., Bledowski et al., 2006; Todd, Han, Harrison, & Marois, 2011; Wendelken, Bunge, & Carter, 2008). Although the inclusion of the latter group of studies increases the statistical power, it is otherwise problematic because ensuing encoding-, maintenance-, and retrieval-phase datasets differ in several ways that have nothing to do with phase per se, such as stimuli type, task requirement, and reference condition. Therefore, despite some loss in statistical power, I chose to include only studies that reported the activation effects of all three phases, thereby rendering different task-phase data well matched in terms of potential confounding factors. Fortunately, the collected dataset was relatively large even with this restriction, and provided reasonably high statistical power.

In the present study, and likely in some of the previous studies, the ultimate purpose of separating encoding-, maintenance-, and retrieval-phase effects was to evaluate whether and to what extent

different phase effects involve common or distinct neural regions. Although this purpose naturally demands direct comparisons between different phase effects, the vast majority of previous studies that separated three-phase effects did not make such comparisons (e.g., Cairo et al., 2004; Manoach et al., 2003; Passaro et al., 2013; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002). While this practice may merely follow from the goal of these studies not including any comparisons, it necessarily precludes a clear appreciation of which regions are commonly or distinctly involved in different WM phases. Obviously, "visual comparisons" cannot substitute formal inferences based on statistical testing. In this regard, the present study emphasized not only separate meta-analysis of encoding-, maintenance- and retrieval-phase data but also direct comparisons between them.

A large body of evidence now indicates that the brain is organized into multiple large-scale intrinsic networks, each comprising a set of discontinuous but intimately interacting regions (Eickhoff, Yeo, & Genon, 2018; Gordon et al., 2017; Yeo et al., 2011). This evidence resonates with the theoretical stance that WM does not involve a dedicated system, but rather emerges from the interactions among the systems that support more basic functions, such as attention, perception, and action (D'Esposito & Postle, 2015; Eriksson, Vogel, Lansner, Bergström, & Nyberg, 2015; Postle, 2006). Thus, activations during WM tasks can be seen more suitably as components of large-scale networks that act in concert rather than regions responding in isolation. In this regard, an increasing number of recent WM studies have adopted a specific network-based approach (Dagenbach, 2019; Santangelo & Bordier, 2019; Wallis, Stokes, Cousijn, Woolrich, & Nobre, 2015). Based on the global and broad match between intrinsic-network topography and concentrations of WM activations across studies, WM is most closely associated with two intrinsic networks: dorsal attention network (DAN) and frontoparietal control network (FPCN; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008; Yeo et al., 2011). Thus, the present study emphasized these two networks in formulating hypotheses for the meta-analysis and interpreting the results, as described in more detail below.

1.3 | A network-based model of WM stages

Figure 1a shows the major DAN and FPCN regions, along with the terms used to refer to them in this study. The activity of the DAN increases during externally directed cognition, such as stimulus processing, visual orienting, and target detection, suggesting that it embodies a mechanism for orienting attention to the external environment (Corbetta & Shulman, 2002; Fox et al., 2005; Sestieri, Shulman, & Corbetta, 2012). The FPCN shows high activity during executive function tasks, such as conflict resolution, task switching, and decision making, providing evidence that it mediates cognitive control processes (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Niendam et al., 2012; Vincent et al., 2008). A Neurosynth-based decoding of DAN and FPCN regions performed herein supports the notion that they play a strong role in external attention and cognitive control processes, respectively. As Figure 1b illustrates, top semantic associates of the DAN include terms such as "spatial,"

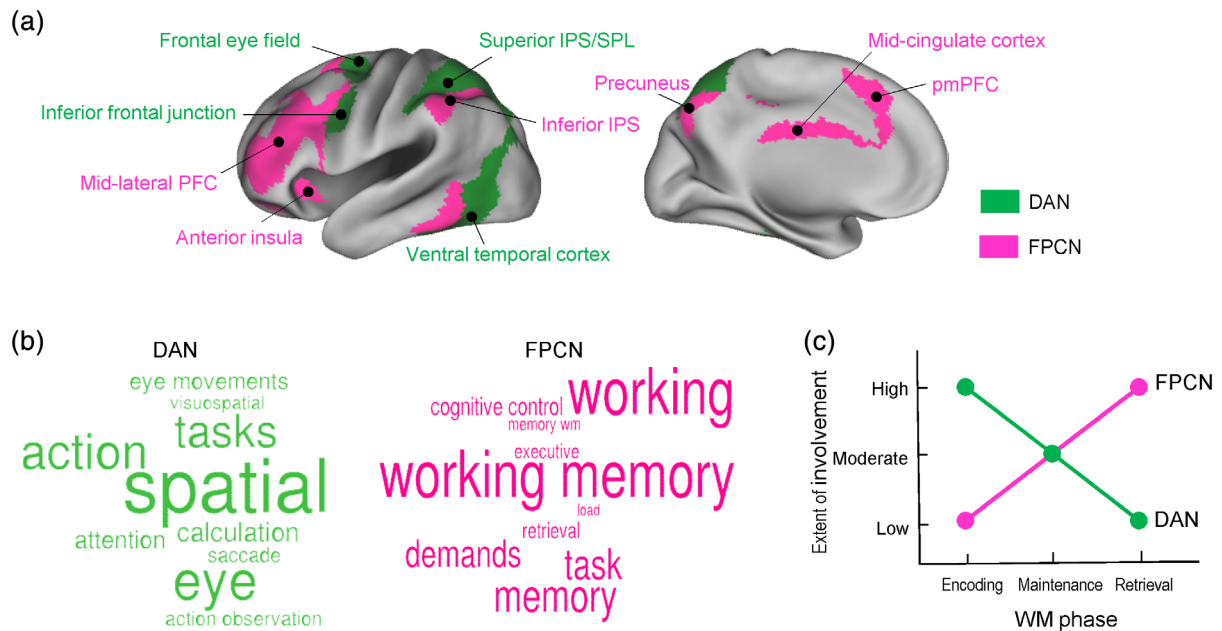


FIGURE 1 (a) Estimates of the dorsal attention network (DAN; shown in green) and the frontoparietal cognitive control network (FPCN; pink), produced using data from Yeo et al. (2011). (b) A Neurosynth function called “decoding” can generate a rank-ordered list of associated terms given an activation image, based on the similarity between the image and a large number of meta-analytic maps (<http://neurosynth.org>; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011). This function was used to extract the top 10 semantic associates of the DAN and FPCN regions shown in (a), which are presented here in word clouds. The size of a term in each cloud is proportional to the strength of similarity. (c) A graphic illustration of the proposed model of intrinsic network involvement in working memory (WM) encoding, maintenance, and retrieval. IPS, intraparietal sulcus; pmPFC, posteromedial prefrontal cortex; SPL, superior parietal lobe [Color figure can be viewed at wileyonlinelibrary.com]

“attention,” “visuospatial,” and “eye movements” and those of the FPCN terms such as “working memory,” “cognitive control,” “executive,” and “demands” (for methodological details, see Figure 1). The DAN and FPCN include many (but not all) of the cortical sites where WM-related activations have been most consistently observed, including the mid-lateral PFC, inferior frontal junction (IFJ), and intraparietal sulcus (IPS). The DAN and FPCN subregions are closely juxtaposed in both frontal and posterior cortices, such as IFJ versus caudal PFC and superior versus inferior IPS, indicating that two very adjacent WM-activations can subserve highly differential functions.

The model of WM stages proposed herein involves the following three core hypotheses:

Hypothesis 1 Encoding is extensively associated with the DAN, but much less with the FPCN.

Hypothesis 2 Maintenance is associated with each of the DAN and FPCN to a moderate extent.

Hypothesis 3 Retrieval is extensively associated with the FPCN, but much less with the DAN.

Figure 1c graphically illustrates these hypotheses. Below, I first discuss the rationale for these hypotheses and then describe additional hypotheses derived from them.

With regard to Hypothesis 1 (encoding), both anecdotal and scientific evidence indicates that attention “gates” or determines what will

be encoded into WM (Gazzaley, 2011; Rutman, Clapp, Chadick, & Gazzaley, 2010; Schmidt, Vogel, Woodman, & Luck, 2002), providing a basis to expect relatively extensive recruitment of the DAN during an encoding phase. In contrast, the FPCN is likely involved more conditionally because its activity scales with the amount and complexity of the memoranda. Given that WM studies typically employ very simple and repetitive stimuli as memoranda, such as letters, digits, and dots (Cairo et al., 2004; Chang, Crottaz-Herbette, & Menon, 2007; Habeck et al., 2005; Manoach et al., 2003; Rowe & Passingham, 2001), an encoding phase may in most cases recruit the FPCN to a relatively weak extent. In sum, an encoding phase may typically recruit the DAN to a greater extent, but the FPCN to a lesser extent.

Hypothesis 2 (maintenance) reflects multiple lines of evidence. First, as regards the involvement of the DAN, previous studies established that orienting attention in, or selecting information from, visual space versus WM involves extensively overlapping regions that are largely within the DAN (Ikka & Curtis, 2011; Nee & Jonides, 2009; Nobre et al., 2004; Tamber-Rosenau, Esterman, Chiu, & Yantis, 2011; for a meta-analysis, see Wallis et al., 2015). Thus, the DAN, perhaps more commonly characterized as “external attention network,” also plays a role in WM-based attentional operations, providing a basis to expect the participation of the DAN in WM maintenance. However, studies also indicated that despite this commonality, some DAN regions were associated more strongly with attentional operations in visual space than in WM (Corbetta, Kincade, & Shulman, 2002; Emrich, Riggall, LaRocque, & Postle, 2013; Nee & Jonides, 2009; Nobre et al., 2004), suggesting that if other things are held

constant, the network tends to be more strongly recruited in the presence than in the absence of stimulus. In this regard, the DAN may be recruited with moderate, rather than high, strength during a maintenance stage. Although the term “moderate” is relatively ambiguous, the strength can be more precisely specified relative to that in other stages, that is, intermediate between the encoding and retrieval stages, as illustrated in Figure 1c. Next, as regards the involvement of the FPCN, keeping information “online” taxes some control-demanding processes such as rehearsal, sustained attention, and distractor resistance (Awh et al., 1999; Chun, 2011; Sakai, Rowe, & Passingham, 2002a). However, given that such processes tend to involve relatively monotonous operations rather than very complex manipulation of information (e.g., decision making, conflict resolution), the FPCN may also be recruited with moderate, rather than high, strength during a maintenance stage. In sum, a maintenance phase may typically recruit each of the DAN and FPCN to a moderate extent.

With regard to Hypothesis 3 (retrieval), a retrieval phase strongly demands executive control functions, such as memory scanning, matching operation involving the sample and probe stimuli, decision making, and response selection (for reviews, see Eriksson et al., 2015; Jonides et al., 2008), which supports the expectation for relatively extensive recruitment of the FPCN during the phase. A retrieval phase also demands external attention because it requires processing of a probe. However, given that externally and internally directed cognition are largely antagonistic to each other (Boly et al., 2007; Dixon, Fox, & Christoff, 2014; Huijbers, Pennartz, Cabeza, & Daselaar, 2009; Kim, 2018), persistent attention to the external environment would interfere with memory scanning, decision making, and other controlled processes that are based on internal representations. Thus, subjects' initial attention to a probe may soon be replaced by more persistent attention to internal representations (of a probe and sample stimuli), which supports the expectation for relatively weak recruitment of the DAN during the phase. Moreover, in trials when a probe is a repeat of a stimulus presented at encoding, neural priming effects, known as “repetition suppression” (for reviews, see Grill-Spector, Henson, & Martin, 2006; Schacter, Wig, & Stevens, 2007) would further constrain activation of the DAN. In sum, a retrieval phase may typically recruit the FPCN to a greater extent, but the DAN to a lesser extent.

The three core hypotheses were used to derive the following six hypotheses:

Hypothesis 4 Regions more strongly associated with encoding than maintenance involve some DAN, but few FPCN, regions, whereas the reverse, that is, the involvement of some FPCN, but few DAN, regions, is true for regions more strongly associated with maintenance than encoding.

Hypothesis 5 Regions more strongly associated with maintenance than retrieval involve some DAN, but few FPCN, regions, whereas the reverse is true for regions more strongly associated with retrieval than maintenance.

Hypothesis 6 Regions more strongly associated with encoding than retrieval involve some DAN, but few FPCN, regions, whereas the reverse is true for regions more strongly associated with retrieval than encoding.

Hypothesis 7 Regions common to encoding and maintenance involve the DAN to a greater extent, but the FPCN to a lesser extent.

Hypothesis 8 Regions common to maintenance and retrieval involve the FPCN to a greater extent, but the DAN to a lesser extent.

Hypothesis 9 Regions common to encoding and retrieval involve both the DAN and FPCN to a limited extent.

Hypotheses 4 through 6 address the distinct substrates of different WM phases and Hypotheses 7 through 9 address the common substrates. I will not further dwell on these hypotheses because they can be seen largely as logical extensions of the three core hypotheses.

To summarize, the proposed model comprises nine hypotheses regarding the recruitment of the DAN and FPCN during three WM stages and their shared and distinct effects. In essence, it suggests that the transition from the encoding to maintenance and to retrieval stages involves progressively decreasing involvement of the DAN, but progressively increasing involvement of the FPCN. Although the model is broadly specified in terms of whole networks rather than their constituent components, this limitation does not prevent the model from providing a useful framework for further research efforts on related topics.

2 | MATERIALS AND METHODS

2.1 | Data collection

Candidate studies employed functional magnetic resonance imaging (fMRI) as the imaging modality and various delayed-response tasks as the behavioral paradigm. Positron emission tomography studies were not considered for inclusion, because specific separation of different task phases requires an event-related design. To identify candidate studies, the PubMed database was searched on July 7, 2018, with the search strings: “fMRI AND ‘working memory’ AND (encoding OR maintenance OR retrieval OR Sternberg OR ‘delayed match to sample’ OR ‘delayed simple matching’)”. In addition, the reference sections from relevant meta-analysis studies (e.g., Rottschy et al., 2011; Wager & Smith, 2003; Wang et al., 2019) were screened to identify studies not identified by the online database search. Search results were filtered to include only studies that met the following inclusion/exclusion criteria:

1. Only studies that tested healthy subjects with no sign of mental or neurological illness were included.
2. Only studies that involved the presentation of stimuli through a visual modality were included.
3. Only studies that reported whole-brain data and peak activation foci in standard stereotaxic coordinates (i.e., Talairach or Montreal Neurological Institute [MNI]) were included.

4. Only studies that reported activation effects of all three phases were included (see section 1 for the rationale for this criterion).
5. A few studies employed a design that involved the presentation of external stimuli during a maintenance phase, such as distractors. These studies were excluded to guard against the potential confounding of maintenance-related effects with perceptually driven ones.
6. A few studies reported multiple activation contrasts of similar types, such as load 5 > load 3 and load 3 > load 1. In each of these studies, only one contrast was included to keep that study from overly affecting the results. The activation contrast that involved the highest number of peak activation foci was selected, based on the rationale that it would maximize the sensitivity of the meta-analysis.
7. Deactivation data (e.g., baseline > WM task) were excluded because such data have been rarely reported and are not directly related to the present hypotheses.

2.2 | Sample characteristics

Forty-seven studies met the inclusion/exclusion criteria and were included in the meta-analysis. These studies are listed in Table 1 by authors and year of publication, along with information regarding the number of subjects, composition of activation contrast, stimuli type, retrieval task, and the number of foci. The mean number of subjects per study was 17.7 ($SD = 10.1$). Behavioral performance was in the good to excellent range in most included studies. Of 32 studies that numerically reported the proportion of correct responses, it was in 0.90 s in 14, 0.80 s in 12, 0.70 s in 3, and <0.70 s in 3. Thus, this study may involve possible biasing effects linked to poor behavioral performance to a minimal degree. The composition of activation contrast was task > baseline in 20 experiments, load-related increase in 11, task > sensorimotor control in 8, difficult condition > easy condition (e.g., manipulation > no-manipulation) in 6, and correct-response trials > incorrect-response trials in 2. The stimuli type was verbal (letters, words, numbers) in 25 experiments, abstract shapes (e.g., dots, polygons) in 13, concrete objects (e.g., faces, scenes) in 7, and a combination of verbal and shape stimuli in 2. The retrieval task was identity verification in 28 experiments, location verification or recall in 6, both identity and location verification in 6, order verification in 2, and other operations (e.g., verbal recall, semantic verification) in 5. The delay-period interval was fixed (e.g., 5 s) in 32 experiments and variable (e.g., 4, 8, 12 s) in 15. The mean number of foci was 11.2 ($SD = 7.2$) for encoding, 9.5 ($SD = 6.6$) for maintenance, and 11.6 ($SD = 8.8$) for retrieval conditions.

2.3 | Meta-analysis

Three sets of meta-analyses were performed. First was a series of single-study meta-analyses that separately evaluated each phase effect, namely, encoding, maintenance, and retrieval. The second was a series of pairwise subtraction analyses between different phase effects to evaluate the extent to which they involved distinct regions. The third was a series of pairwise conjunction analyses between different phase effects to evaluate the extent to which they involved

similar regions. All analyses were conducted using the activation likelihood estimation (ALE) algorithm (Eickhoff et al., 2009; Turkeltaub et al., 2012) implemented in the software program GingerALE 3.0.2 (<http://www.brainmap.org>). ALE is a peak-coordinate-based meta-analysis approach that can be used to estimate above-chance activation convergence across independent studies. The ALE algorithm was applied to analyze the present data in the following steps (I have previously described similar methodological steps in Kim (2019) and other similar studies).

All activation coordinates reported in the Talairach space were converted to the MNI space using the GingerALE transformation algorithm. The reported foci for each study were modeled as the centers of 3-dimensional (3D) Gaussian probability distributions, thereby accounting for the spatial uncertainty associated with each focus. The size of the full-width at half maximum (FWHM) of the Gaussian kernel was not manually specified, but determined by an extended ALE algorithm which weighted, among other things, the individual sample size, to accommodate the fact that larger sample sizes provide more certain estimates of the true spatial locations. As an example, the meta-analysis of the encoding-phase data involved minimum, median, and maximum FWHM values of 8.73, 9.50, and 10.94 mm, respectively. The 3D Gaussian probability values were combined across all of the reported foci in a given study and then across all of the studies included in the meta-analysis, thereby estimating the likelihood of activation at every voxel. These ALE values were tested against the null hypothesis of a uniform distribution of foci, using a cluster-level, familywise error (FWE)-corrected threshold of $p < .05$ with a cluster-forming, voxel-level threshold of $p < .005$.

A conjunction analysis between two ALE maps was performed based on the intersection between the two thresholded maps. Thus, a voxel determined to be significant in a conjunction analysis survived a cluster-level, FWE-corrected threshold of $p < .05$ with a cluster-forming, voxel-level threshold of $p < .005$ in both ALE analyses. A spatial extent threshold exceeding 500 mm^3 was imposed to further constrain the possibility of false-positive findings. To conduct a subtraction analysis between two ALE maps, all studies contributing to either map were combined and randomly split into two groups of the same size as the original two groups. Voxel-wise ALE values for these two randomly formed groups were computed and subtracted from each other. Repeating this process 10,000 times created an expected distribution of ALE-value differences under the null hypothesis. The observed differences in the ALE scores were tested against this null distribution, using a voxel-wise threshold of $p < .05$. A correction for multiple comparisons was not applied to a subtraction analysis because (a) the present approach is largely hypothesis-driven, (b) between-phase differences were expected to be relatively subtle in the magnitude given that they referred to within-trial effects, and (c) the possibility of false-positive findings was further constrained by a spatial extent threshold exceeding 500 mm^3 .

To visualize the meta-analysis results, the thresholded ALE maps were projected onto the inflated surface of a population-average, and landmark- and surface-based (PALS) atlas by using the Caret software suite (Van Essen, 2005). To visualize the subcortical structures not

TABLE 1 Overview of studies included in the present meta-analysis

Study	Subjects	Contrast	Stimulus	Task	Foci		
					E	M	R
Beatty et al., 2015	43	Task > baseline	Shapes	Identity verification	4	3	3
Bedwell et al., 2005	14	Task > control	Letters	Identity verification	19	24	10
Bennett, Rivera, & Rypma, 2013	42	Load-related increase	Letters	Identity verification	5	10	2
Bergmann, Daselaar, Fernandez, & Kessels, 2016	24	Correct > incorrect	Objects/scenes	Location verification	0	7	15
Bokde et al., 2010	8	Task > baseline	Letters	Identity verification	18	8	17
Cairo et al., 2004	18	Task > baseline	Letters	Identity verification	19	12	18
Chang et al., 2007	14	Load-related increase	Numbers	Identity verification	11	31	9
Chein & Fiez, 2001	12	Task > baseline	Words	Verbal recall	13	10	15
Chen & Desmond, 2005	15	Load-related increase	Letters	Identity verification	37	14	12
Curtis, Rao, & D'Esposito, 2004	15	Difficult > easy	Shapes	Oculomotor-based location recall	2	7	7
de Leeuw, Kahn, Zandbelt, Widschwendter, & Vink, 2013	24	Task > control	Letters	Identity verification	16	7	14
de Leeuw et al., 2013	24	Task > control	Letters	Identity verification	13	9	10
Fiebach, Friederici, Smith, & Swinney, 2007	12	Difficult > easy	Words	Semantic verification	0	1	3
Fiehler et al., 2011	21	Task > baseline	Shapes	Grasping-based shape recall	7	3	7
Gibbs & D'Esposito, 2005a	10	Task > baseline	Shapes	Identity/location verification	8	8	15
Gibbs & D'Esposito, 2005b	13	Task > baseline	Letters	Identity verification	14	5	17
Gibbs & D'Esposito, 2006	9	Task > baseline	Shapes	Identity/location verification	6	3	15
Grot et al., 2017	23	Difficult > easy	Words/shapes	Location verification	9	5	0
Habeck et al., 2005	40	Load-related increase	Letters	Identity verification	8	22	10
Jenness et al., 2018	54	Task > baseline	Faces/scenes	Identity verification	5	9	2
Karlsgodt, Shirinyan, van Erp, Cohen, & Cannon, 2005	13	Task > baseline	Words	Identity verification	14	8	16
Klaassen et al., 2013	21	Load-related increase	Letters	Identity verification	14	15	8
Kochan et al., 2011	18	Load-related increase	Shapes	Identity/location verification	6	7	10
Kondo, Nomura, & Kashino, 2015	28	Task > baseline	Shapes	Location verification	11	9	5
Lagopoulos, Ivanovski, & Malhi, 2007	10	Load-related increase	Words	Identity verification	7	17	11
Landau, Lal, O'Neil, Baker, & Jagust, 2009	23	Load-related increase	Letters	Identity verification	24	12	1
Landau, Schumacher, Garavan, Druzgal, & D'Esposito, 2004	10	Task > baseline	Faces	Identity verification	6	2	8
Luck et al., 2010	17	Task > baseline	Letters/shapes	Identity/location verification	12	4	14
Majerus et al., 2013	21	Task > control	Words	Identity verification	14	0	27
Manoach et al., 2003	12	Task > baseline	Numbers	Identity verification	20	11	49
Marvel & Desmond, 2010	16	Difficult > easy	Letters	Identity verification	21	21	5
Mohr, Goebel, & Linden, 2006	13	Difficult > easy	Shapes	Color/angle verification	20	20	11
Narayanan et al., 2005	12	Task > baseline	Letters	Identity verification	12	8	16
Panwar et al., 2014	18	Task > baseline	Words	Identity verification	7	5	5
Passaro et al., 2013	10	Task > baseline	Shapes	Identity/location verification	8	16	13
Pessoa et al., 2002	9	Correct > incorrect	Shapes	Identity verification	9	9	9
Rämä & Courtney, 2005	12	Task > control	Faces	Identity verification	11	12	17
Ravizza, Hazeltine, Ruiz, & Zhu, 2011	17	Load-related increase	Letters	Order verification	3	4	1
Röder, Mohr, & Linden, 2011	22	Load-related increase	Faces	Identity/emotion verification	11	5	3

(Continues)

TABLE 1 (Continued)

Study	Subjects	Contrast	Stimulus	Task	Foci		
					E	M	R
Ross, LoPresti, Schon, & Stern, 2013	16	Difficult > easy	Faces	Identity verification	1	4	36
Rowe & Passingham, 2001	6	Task > baseline	Shapes	Joystick-based location recall	12	5	14
Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000	6	Task > control	Shapes	Joystick-based location recall	4	5	7
Rypma & D'Esposito, 2000	25	Task > baseline	Letters	Identity verification	18	9	19
Sakai, Rowe, & Passingham, 2002b	12	Task > control	Letters	Order verification	4	11	6
Sayala, Sala, & Courtney, 2006	10	Task > control	Faces	Identity/location verification	22	14	12
Sheridan, Hinshaw, & D'Esposito, 2007	10	Task > baseline	Letters	Identity verification	8	0	12
Taylor et al., 2004	10	Load-related increase	Shapes	Identity verification	12	16	7

Abbreviations: E, encoding; M, maintenance; R, retrieval.

visible on the PALS atlas, the thresholded ALE maps were also imported into the Mango software program (<http://ric.uthscsa.edu/mango>) as an overlay on an International Consortium for Brain Mapping template. Yeo et al. (2011) parcellated the cerebral cortex region into seven intrinsic networks based on functional connectivity analyses of resting-state data. Estimated boundaries of the DAN and FPCN in this study (Figure 1a) were also projected onto the PALS to evaluate whether convergence clusters were located inside or outside these networks. These boundaries were used as flexible guidelines rather than fixed templates, with the understanding that intrinsic network boundaries are dynamically organized rather than strictly fixed, as discussed in more detail below.

2.4 | Conjunction analysis between WM-phase maps and Yeo 7 networks

To further evaluate the present model, a conjunction analysis was performed between WM-phase maps and Yeo et al.'s (2011) 7 networks (data available from https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation_Yeo2011), using the Mango software program. For each WM-phase map, this analysis indicated what percentage of it overlaps with the DAN, FPCN, and other networks. The advantages of Yeo 7-network model, relative to other similar models of brain parcellation, are that it is built on a large dataset ($n = 1,000$), it involves an extensive range of validation efforts, including a split-half replication, its topography corresponds closely to that of activation maps observed in subtraction imaging studies, and its usefulness as a frame of reference in interpreting task-based activations has been repeatedly demonstrated (e.g., Benoit & Schacter, 2015; Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015; Kim, 2015, 2018; Rosen, Stern, Michalka, Devaney, & Somers, 2016). However, any resting state-based connectivity models are at best an approximate framework for interpreting task-based fMRI activations, because functional coupling across dispersed brain regions differs between rest and task, although overall network configuration remains preserved (Buckner, Krienen, & Yeo, 2013; Gonzalez-Castillo & Bandettini, 2018; Krienen, Yeo, & Buckner,

2014). Thus, the breakdown of WM-phase maps as a function of Yeo 7 networks was meant to aid in interpreting meta-analysis results rather than to test the model in a rigorously quantitative way.

2.5 | Neurosynth-based decoding of WM-phase maps

Neurosynth is a meta-analytic platform comprising over 14,000 published fMRI studies and over 1,300 topic terms (<http://neurosynth.org>). A Neurosynth function called "decoding" can generate a rank-ordered list of associated terms given an activation image in standard space, based on similarity coefficients (Pearson r) between the input image and a large number of meta-analytic maps (Yarkoni et al., 2011). This function was used herein to decode WM-phase maps, with the general expectation that some terms would be common to all phase maps, reflecting anatomical overlaps between them, whereas others would be more specific to each map, reflecting anatomical differentiation between them. This analysis was performed with the following restrictions. First, anatomical terms were excluded from a list to focus on image-to-function, as opposed to image-to-anatomy, decoding. Second, when a list had multiple terms having the same base, only the one with the highest-ranking was included. For each decoding, "task-tasks" was the only instance to which this rule was actually applied. Third, to strike a balance between sensitivity and specificity of decoding, only the top 10 strongest associates were examined in detail for each decoding. Finally, decoding of unthresholded and thresholded maps yielded highly comparable results, but similarity coefficients were generally greater for the former. Thus, only the results based on unthresholded maps are reported below.

3 | RESULTS

3.1 | Encoding-, maintenance-, and retrieval-phase effects

Table 2 shows the results of the separate ALE meta-analyses of different phase effects. Figures 2 and 3 illustrate above-threshold cortical

TABLE 2 Results of separate ALE meta-analyses of encoding-, maintenance-, and retrieval-phase effects

Volume (mm ³)	MNI			ALE	Region
	x	y	z		
<i>Encoding</i>					
8,496	-24	-68	40	0.029	Left superior IPS, SPL
6,512	-48	-6	50	0.033	Left IFJ, PCG
6,176	-4	2	62	0.039	Left pmPFC, bilateral SMA
5,808	16	-68	56	0.024	Right superior IPS, SPL
4,864	48	6	28	0.030	Right IFJ, PCG
3,128	-18	10	2	0.031	Left striatum
<i>Maintenance</i>					
15,560	-4	4	58	0.055	Bilateral pmPFC, SMA
	-54	-4	44	0.026	Left frontal eye field, PCG
8,944	-28	-64	42	0.030	Left superior/inferior IPS
7,128	-30	24	4	0.029	Left anterior insula, FO
	-20	10	-6	0.028	Left striatum
4,768	38	42	26	0.028	Right mid-lateral PFC
3,600	-54	8	28	0.021	Left mid-lateral PFC, IFJ
3,208	46	-44	46	0.032	Right superior/inferior IPS
2,920	36	26	-6	0.027	Right anterior insula, FO
2,088	26	6	56	0.022	Right dorsal caudal PFC
<i>Retrieval</i>					
11,384	-4	8	50	0.037	Bilateral pmPFC, SMA
8,256	-48	12	28	0.033	Left mid-lateral PFC, IFJ
6,976	34	24	-2	0.047	Right anterior insula, FO
6,296	-32	24	-4	0.048	Left anterior insula, FO
2,528	-30	-56	38	0.018	Left superior/inferior IPS
2,024	-12	-16	4	0.028	Left thalamus

Abbreviations: FO, frontal operculum; IFJ, inferior frontal junction; IPS, intraparietal sulcus; PCG, precentral gyrus; pmPFC, posteromedial PFC; SMA, supplementary motor area; SPL, superior parietal lobe.

and subcortical regions, respectively. Consistent with Hypothesis 1, the encoding phase involved many DAN regions, that is, bilateral IFJ and bilateral superior IPS/superior parietal lobe, but only one FPCN region, that is, left posteromedial PFC (pmPFC; see Figure 2a). Outside the DAN and FPCN, it mainly involved the bilateral supplementary motor area (SMA) and left striatum regions.

Consistent with Hypothesis 2, the maintenance phase involved many DAN regions, that is, left IFJ, left frontal eye field, and bilateral superior IPS, and also many FPCN regions, that is, bilateral mid-lateral PFC, anterior insula, pmPFC, and inferior IPS (Figure 2b). Outside the DAN and FPCN, it mainly involved the bilateral SMA, bilateral frontal operculum, and left striatum regions.

Consistent with Hypothesis 3, the retrieval phase involved many FPCN regions, that is, left mid-lateral PFC, bilateral anterior insula, bilateral pmPFC, and left inferior IPS, but only two DAN regions, that is, left IFJ and superior IPS (Figure 2c). Outside the DAN and FPCN, it mainly involved the bilateral SMA, bilateral frontal operculum, and left thalamus regions.

3.2 | Pairwise subtraction analyses

Table 3 and Figure 4 show the results of pairwise subtraction analyses between different phase effects. A subtraction analysis between encoding and maintenance effects indicated a double dissociation consistent with Hypothesis 4. Specifically, preferential encoding effects indicated two DAN regions, that is, right IFJ and left superior IPS, but no FPCN region. In contrast, preferential maintenance effects indicated many FPCN regions, that is, right mid-lateral PFC, left pmPFC, bilateral anterior insula, and bilateral inferior IPS, but no DAN region (Figure 4a). Outside the DAN and FPCN, preferential encoding effects involved no above-threshold region, and preferential maintenance effects mainly involved the right frontal operculum area.

A subtraction analysis between maintenance and retrieval effects indicated a double dissociation consistent with Hypothesis 5, with only one minor area of exception. Specifically, preferential maintenance effects involved two DAN regions, that is, left frontal eye field and superior IPS, and one minor FPCN region, that is, right dorsal

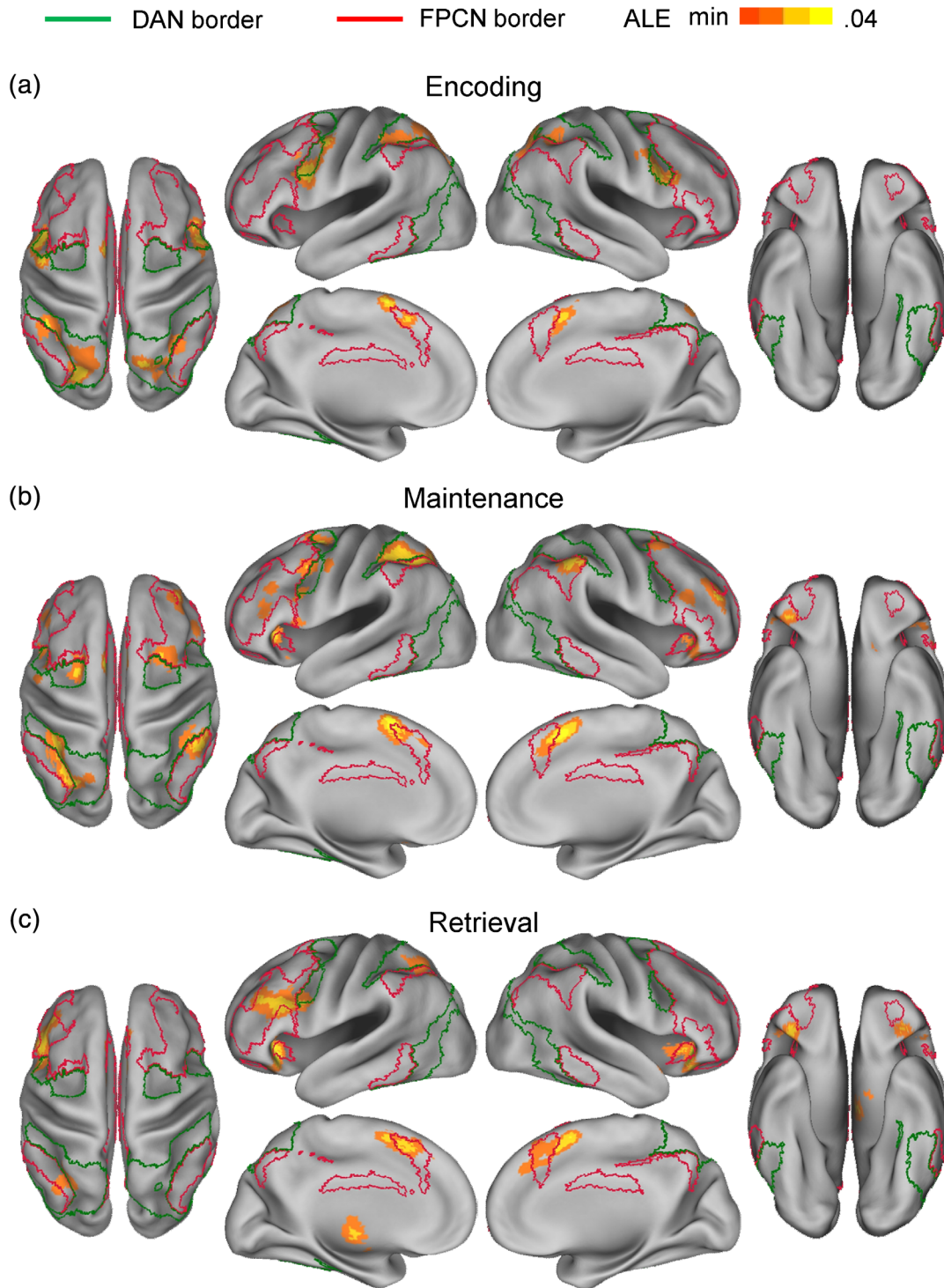


FIGURE 2 Above-threshold regions in separate ALE meta-analyses of (a) encoding-, (b) maintenance-, and (c) retrieval-phase data. Green and crimson lines indicate estimated boundaries of the dorsal attention network (DAN) and the frontoparietal control network (FPCN) in Yeo et al.'s (2011) 7-network model, respectively. NIFTI files available at <https://identifiers.org/neurovault.collection:5506> [Color figure can be viewed at wileyonlinelibrary.com]

caudal PFC. In contrast, preferential retrieval effects involved many FPCN regions, that is, left mid-lateral PFC, bilateral pmPFC, and bilateral anterior insula (Figure 4b). Outside the DAN and FPCN, preferential maintenance effects mainly involved the left SMA and striatum regions, and preferential retrieval effects mainly involved the bilateral frontal operculum and left thalamic regions.

A subtraction analysis between encoding and retrieval effects indicated a double dissociation consistent with Hypothesis 6. Specifically, preferential encoding effects involved many DAN regions, that is, right IFJ and bilateral superior IPS/superior parietal lobe, but no FPCN region. In contrast, preferential retrieval effects involved many FPCN regions, that is, left mid-lateral PFC, bilateral pmPFC, and bilateral

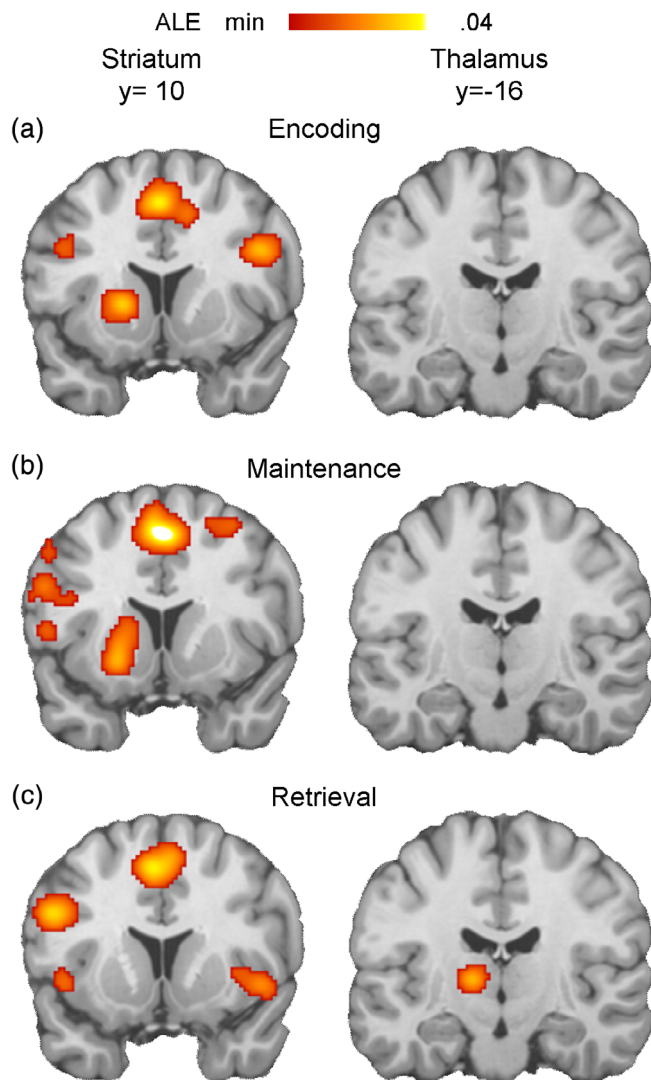


FIGURE 3 Above-threshold subcortical regions in separate ALE meta-analyses of (a) encoding-, (b) maintenance-, and (c) retrieval-phase data [Color figure can be viewed at wileyonlinelibrary.com]

anterior insula, but no DAN region (Figure 4c). Outside the DAN and FPCN, preferential encoding effects mainly involved the left SMA and striatum regions, and preferential retrieval effects mainly involved the bilateral frontal operculum and left thalamic regions.

3.3 | Pairwise conjunction analyses

Table 4 and Figure 5 show the results of pairwise conjunction analyses between different phase effects. Consistent with Hypothesis 7, encoding and maintenance effects commonly involved many DAN regions, that is, left IFJ and left superior IPS/superior parietal lobe, but only one FPCN region, that is, left pmPFC (Figure 5a). Outside the DAN and FPCN, they commonly involved the bilateral SMA and left striatum regions.

Consistent with Hypothesis 8, maintenance and retrieval effects commonly involved many FPCN regions, that is, left mid-lateral PFC, bilateral anterior insula, bilateral pmPFC, and left inferior IPS, but only

two DAN regions, that is, left IFJ and superior IPS (Figure 5b). Outside the DAN and FPCN, they commonly involved the bilateral SMA and right frontal operculum regions.

Consistent with Hypothesis 9, encoding and retrieval effects commonly involved only two DAN regions, that is, left IFJ and superior IPS, and only one FPCN region, that is, left pmPFC (Figure 5c). Outside the DAN and FPCN, they commonly involved the bilateral SMA region.

3.4 | Association of WM-phase maps with Yeo 7 networks

Table 5 shows a breakdown of WM-phase maps as a function of Yeo 7 networks. Network-composition of each map was generally consistent with the present model. First, consistent with Hypothesis 1, the encoding map overlapped more extensively with the DAN than the FPCN (52.7 vs. 13.7%). Second, consistent with Hypothesis 2, the maintenance map overlapped more equally with the DAN and FPCN (25.6 vs. 41.1%). Third, consistent with Hypothesis 3, the retrieval map overlapped more extensively with the FPCN than the DAN (40.6 vs. 8.6%). Fourth, consistent with the model, overlaps of the phase maps with the DAN progressively decreased from the encoding (52.7%) to maintenance (25.6%) and to retrieval (8.6%) stages. Fifth, also consistent with the model, overlaps with the FPCN increased from the encoding (13.7%) to maintenance (41.1%) stages. However, they did not increase from the maintenance (41.1%) to retrieval (40.6%) stages, providing a potentially important exception to the model. While retrieval involved more regions within the frontal components of the FPCN than maintenance, the reverse was true for the inferior IPS component of the FPCN (compare Figure 2b,c), producing relatively equal overlaps of the two maps with the whole FPCN.

Aside from the DAN and FPCN, the ventral attention network (VAN) was the only network that showed substantial overlaps with each WM-phase map. As Figure 6 illustrates, these within-VAN effects were mostly in the SMA and frontal operculum regions and co-extensive with adjacent FPCN effects involving the pmPFC and anterior insula. While these regions may act in concert with the VAN during a resting state, they may interact more closely with the FPCN than the VAN during the WM task state (and also likely during other cognitively intensive task states), as discussed in more detail below.

3.5 | Image-to-text decoding of WM-phase maps

Table 6 shows the results of the Neurosynth-based decoding of WM-phase maps. Three findings were notable. First, all phase maps were commonly associated with three very general, task-related terms, that is, "tasks," "goal," and "demands," consistent with the hypothesis that WM-related regions serve multiple cognitive, not just WM, demands. Second, all phase maps were also commonly associated with three WM-related terms, that is, "working memory," "working," and "load," indicating the presence of a degree of similarity between Neurosynth-based automatic versus current, annotated meta-analysis of WM-related studies. Finally, most of the other terms were specific to each

Volume (mm ³)	MNI			Z	Region
	x	y	z		
<i>Encoding > maintenance</i>					
1,800	-24	-76	34	3.72	Left superior IPS
1,752	45	5	24	3.35	Right IFJ
<i>Maintenance > encoding</i>					
1,288	-28	24	8	2.77	Left anterior insula, FO
1,016	-32	-60	42	2.37	Left inferior IPS
976	32	28	-8	2.40	Right anterior insula, FO
784	46	24	20	2.89	Right mid-lateral PFC
632	52	-44	48	2.42	Right inferior IPS
592	-14	6	54	2.35	Left pmPFC
<i>Maintenance > retrieval</i>					
3,064	-12	4	62	3.35	Left SMA
	-24	-2	46	2.86	Left frontal eye field
2,296	-35	-47	44	2.77	Left superior IPS
904	-18	12	-8	2.19	Left striatum
712	-52	-10	50	2.74	Left PCG
632	24	6	52	2.52	Right dorsal caudal PFC
<i>Retrieval > Maintenance</i>					
2,952	37	12	-8	3.89	Right anterior insula, FO
2,040	-30	23	-8	3.89	Left anterior insula, FO
888	-46	10	32	2.29	Left mid-lateral PFC
768	2	28	28	2.95	Right pmPFC
704	-8	-30	0	3.29	Left thalamus
672	2	28	58	2.62	Bilateral pmPFC
<i>Encoding > retrieval</i>					
3,352	-22	-76	42	3.54	Left superior IPS, SPL
2,616	20	-68	60	3.29	Right superior IPS, SPL
2,336	56	3	46	3.54	Right IFJ, PCG
2,032	-51	-8	52	3.89	Left PCG
856	-18	6	8	2.26	Left striatum
856	-8	2	66	2.49	Left SMA
<i>Retrieval > encoding</i>					
4,536	34	23	-14	3.89	Right anterior insula, FO
3,840	-37	21	-10	2.99	Left anterior insula, FO
3,440	-49	19	23	3.89	Left mid-lateral PFC
1,488	0	32	26	3.72	Bilateral pmPFC
1,096	2	26	54	2.55	Bilateral pmPFC
672	-14	-10	4	2.54	Left thalamus

TABLE 3 Results of pairwise subtraction analyses among encoding-, maintenance-, and retrieval-phase effects

For abbreviations, see Table 2.

stage. Specific terms for the encoding map included vision- and attention-related terms such as “visual,” “attentional,” and “eye,” consistent with the hypothesis that this phase greatly demands external attention. Specific terms for the maintenance map included WM-related terms such as “memory wm” and “maintenance” and also the

term “phonological,” suggesting that this phase may typically recruit verbal rehearsal operation. Specific terms for the retrieval map included control demand-related terms such as “difficulty,” “task difficulty,” and “verbal,” consistent with the hypothesis that this phase taxes cognitive control processes to a strong extent.

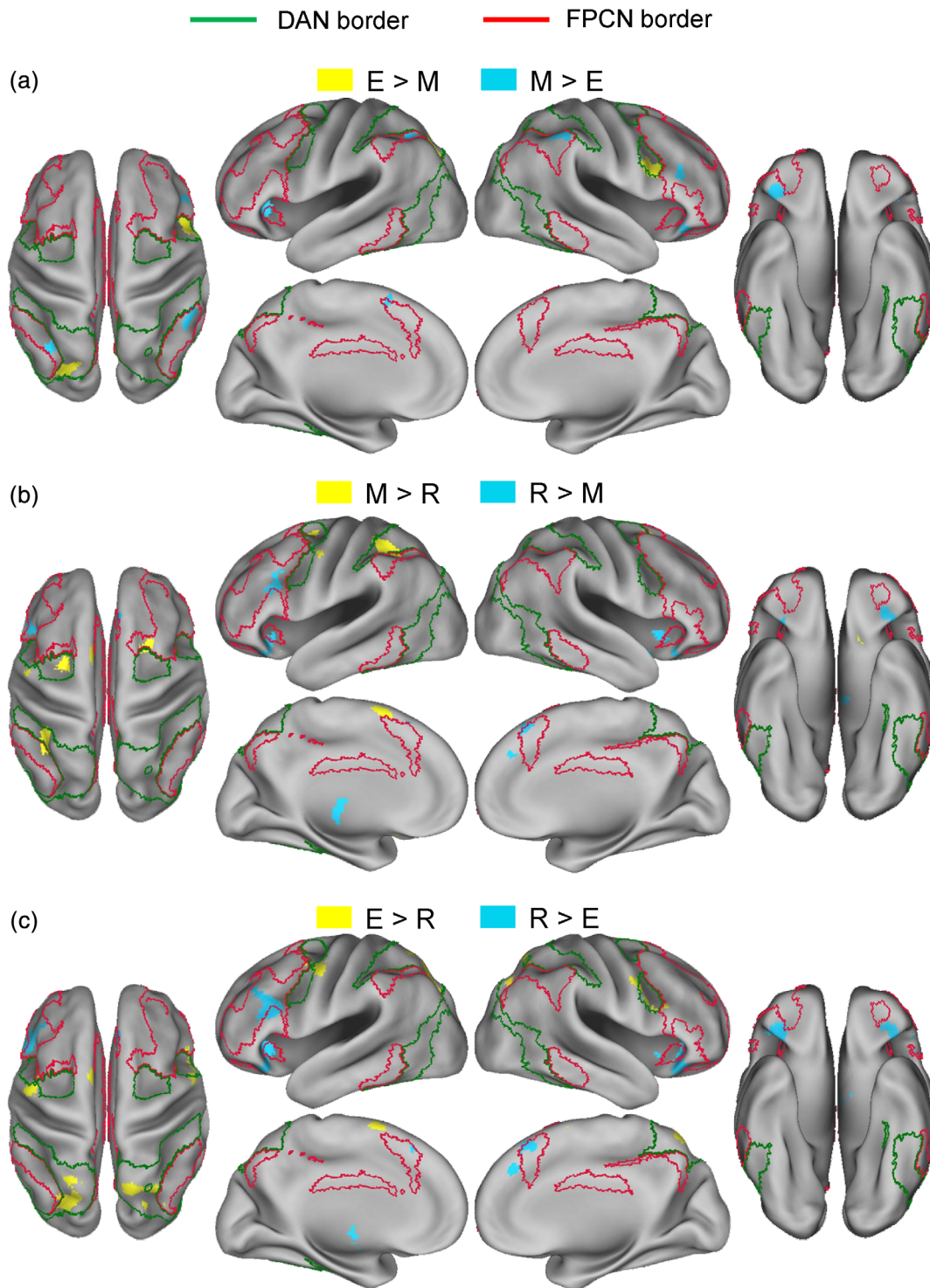


FIGURE 4 Above-threshold regions in a pairwise subtraction analysis between encoding (E), maintenance (M), and retrieval (R) ALE results [Color figure can be viewed at wileyonlinelibrary.com]

3.6 | Supplementary analysis

A criticism of a meta-analysis is that it integrates studies with largely different experimental parameters, thereby producing no easily interpretable results. To address this potential limitation, I additionally performed a subgroup meta-analysis, including only studies that required identity verification of verbal memoranda ($n = 20$) and using a

relatively lenient statistical threshold (voxel-level, $p < .005$, uncorrected; spatial extent, $< 1,000 \text{ mm}^3$). Essential results of this analysis were very similar to those of the main analysis. As illustrated in Figure S1 available online, the encoding phase was more extensively associated with the DAN than the FPCN; the maintenance phase was more equally associated with the two networks; and the retrieval phase involved the FPCN to a greater extent than the DAN.

Volume (mm ³)	MNI			ALE	Region
	x	y	z		
<i>Encoding ∩ maintenance</i>					
4,880	-4	2	62	0.039	Left pmPFC, bilateral SMA
3,000	-26	-66	42	0.023	Left superior IPS
1,816	-18	12	0	0.024	Left striatum
1,616	-54	-2	46	0.025	Left PCG
616	-52	6	26	0.016	Left IFJ
<i>Maintenance ∩ retrieval</i>					
6,704	-4	8	50	0.037	Bilateral pmPFC, SMA
2,304	-54	8	28	0.021	Left mid-lateral PFC, IFJ
2,280	36	26	-6	0.027	Right anterior insula, FO
1,704	-30	-56	38	0.018	Left superior/inferior IPS
1,536	-30	24	4	0.029	Left anterior insula, FO
840	-46	16	0	0.020	Left anterior insula, FO
<i>Encoding ∩ retrieval</i>					
4,000	-2	10	50	0.036	Left pmPFC, bilateral SMA
1,800	-48	6	28	0.026	Left IFJ
728	-28	-56	48	0.018	Left superior IPS

For abbreviations, see Table 2.

Subcortical effects were limited largely to the striatum at encoding and maintenance, but to the thalamus at retrieval. Thus, essential results of the main analysis are unlikely to strongly reflect possible biasing effects linked to heterogeneity of included studies.

4 | DISCUSSION

4.1 | Contribution of the DAN and FPCN to the encoding phase

The encoding phase was associated extensively with the DAN, but only slightly with the FPCN. Specifically, within the DAN, it involved the bilateral IFJ and superior IPS/superior parietal lobe regions to a strong extent, but within the FPCN, only a small portion of the left pmPFC region. Because an encoding phase requires attention to sample stimuli, the involvement of the DAN in the phase adds to existing evidence that the network plays a strong role in external attention (Corbetta & Shulman, 2002; Fox et al., 2005; Sestieri et al., 2012). Despite its close association with the DAN, the encoding phase did not specifically involve its ventral temporal component. Given that this region is part of the “what” pathway, the absence of its involvement may partly reflect the fact that WM studies typically employed very simple and repetitive stimuli. Consistent with this hypothesis, previous studies that presented perceptually more complex stimuli, such as faces and scenes, indicated activation of the region (Jenness et al., 2018; Landau et al., 2004; Rämä & Courtney, 2005; Röder et al., 2011; Sayala et al., 2006). On a related note, studies on long-term memory encoding consistently indicated involvement of the ventral temporal cortex, along with other DAN regions (for a meta-analysis, see Kim, 2011). Thus, an important agenda for future studies is to

TABLE 4 Results of pairwise conjunction analyses among encoding-, maintenance-, and retrieval-phase effects

determine whether activation of this visual region during long-term, but not WM, encoding is due to intrinsic differences between memory domains or some extrinsic, procedural factors that have nothing to do with the memory domain per se.

The limited association of encoding with the FPCN suggests that transforming perceptual inputs into WM representations does not rely heavily on executive control functions. In this regard, the pattern is not necessarily consistent with the view that the central executive system controls the flow of information to its slave, storage systems (Baddeley, 2012), but fits more comfortably with the view that memory formation is a “by-product” or direct consequence of attention focused on relevant information (Chun & Johnson, 2011). However, studies that used a parametric variation of memory load indicated corresponding increases in PFC activity at encoding and other phases (Bennett et al., 2013; Kochan et al., 2011; Landau et al., 2009; Ravizza et al., 2011; Röder et al., 2011), consistent with the hypothesis that the strength of the FPCN involvement scales with the amount and complexity of the memoranda. In this regard, the limited association of encoding with the FPCN is attributable partly to the use of perceptually impoverished stimuli in the majority of previous WM studies.

4.2 | Contribution of the DAN and FPCN to the maintenance phase

The maintenance phase involved the DAN and FPCN to a more equal extent. Specifically, within the DAN, it involved the left IFJ, left frontal eye field, and bilateral superior IPS regions and, within the FPCN, the bilateral mid-lateral PFC, anterior insula, pmPFC, and inferior IPS regions. The involvement of the DAN in the maintenance phase indicates that the network goes beyond subserving attention to external

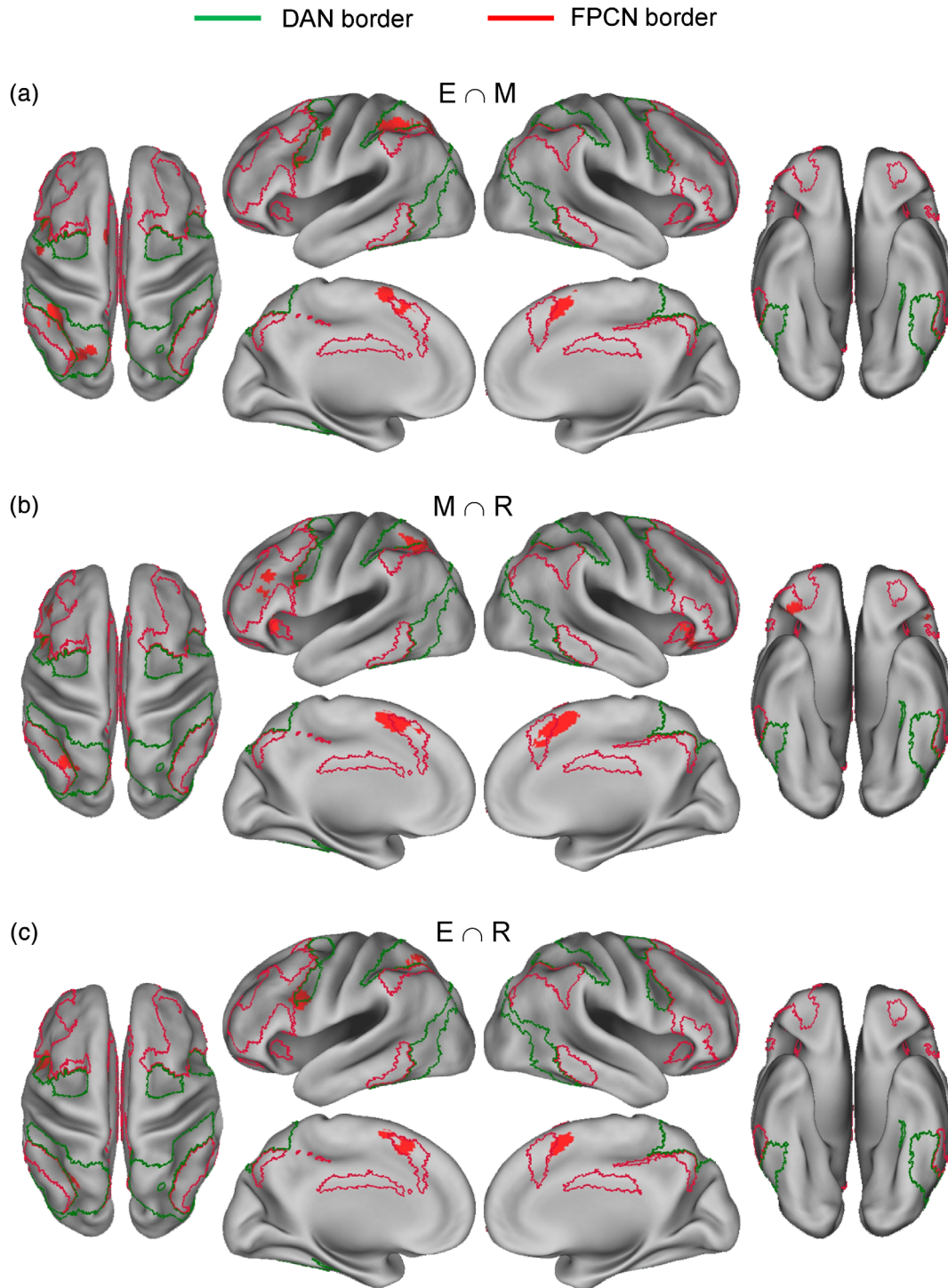


FIGURE 5 Above-threshold regions in a pairwise conjunction analysis between encoding (E), maintenance (M), and retrieval (R) ALE results [Color figure can be viewed at wileyonlinelibrary.com]

information but also plays a role in maintaining information from external sources when the source is no longer present. Previous studies indicated that orienting attention in, or selecting information from, WM involves many regions within the DAN (Ikkai & Curtis, 2011; Nee & Jonides, 2009; Nobre et al., 2004; Tamber-Rosenau et al., 2011; for a meta-analysis, see Wallis et al., 2015), which indirectly suggests a role of the network in WM maintenance. Like the encoding

phase, the maintenance phase did not specifically involve the ventral temporal component of the DAN. Studies using multi-voxel pattern analysis showed decoding of the maintained content in visual areas, even in V1, thereby providing evidence for a sensory recruitment hypothesis of WM (Ester, Serences, & Awh, 2009; Nelissen, Stokes, Nobre, & Rushworth, 2013; Riggall & Postle, 2012; for a review, see Lee & Baker, 2016). Thus, despite the lack of specific supporting

evidence in subtraction-based studies, the ventral temporal region may play some role in representing information in WM.

The involvement of the FPCN in the maintenance phase indicates that maintaining information in WM cannot be supported by the DAN alone, but typically requires an interplay between the DAN and the FPCN. In this regard, the previous literature provided evidence that the PFC plays a strong role in sustained attention to WM and the related function of protecting the information against external interference or task-unrelated thoughts (Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011; Nee et al., 2012; Nichols, Kao, Verfaellie, & Gabrieli, 2006; Sakai et al., 2002a). Studies also indicated that the FPCN is anti-correlated with the default mode network during the maintenance, but not

encoding or retrieval, phase (Piccoli et al., 2015; Santangelo & Bordier, 2019), likely indicating its role in suppressing intrusive thoughts during the delay period (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Dixon et al., 2014). The FPCN may also be required because the DAN alone can only support the maintenance of a very limited amount of information. In this regard, Linden et al. (2003) showed that activity in the lateral PFC and medial frontal regions increased monotonically in response to memory load, even up to the maximum load condition in the study. In contrast, activity in the frontal eye field and IPS regions started to decline as memory load approached the behavioral capacity limit. Other studies (Todd & Marois, 2004; Xu & Chun, 2005) reported comparable dissociations between inferior IPS (FPCN) versus superior IPS (DAN) regions.

TABLE 5 Proportion (%) of encoding-, maintenance-, and retrieval-phase above-threshold regions as a function of Yeo 7 networks

Network	Encoding	Maintenance	Retrieval
Dorsal attention	52.7	25.6	8.6
Frontoparietal control	13.7	41.1	40.6
Ventral attention	20.0	23.3	33.7
Default mode	0.6	4.6	12.3
Visual	2.5	0.0	0.0
Somatomotor	10.4	5.4	3.9
Limbic	0.0	0.0	0.9

4.3 | Contribution of the DAN and FPCN to the retrieval phase

The retrieval phase was associated extensively with the FPCN, but only slightly with the DAN. Specifically, within the FPCN, it involved the left mid-lateral PFC, bilateral anterior insula, bilateral pmPFC, and left inferior IPS regions, but within the DAN, a small portion of left IFJ and superior IPS regions only. Because a retrieval phase almost certainly demands control functions to a great extent, such as memory scanning, matching operation involving the sample and probe stimuli, decision making, and response selection, the strong involvement of

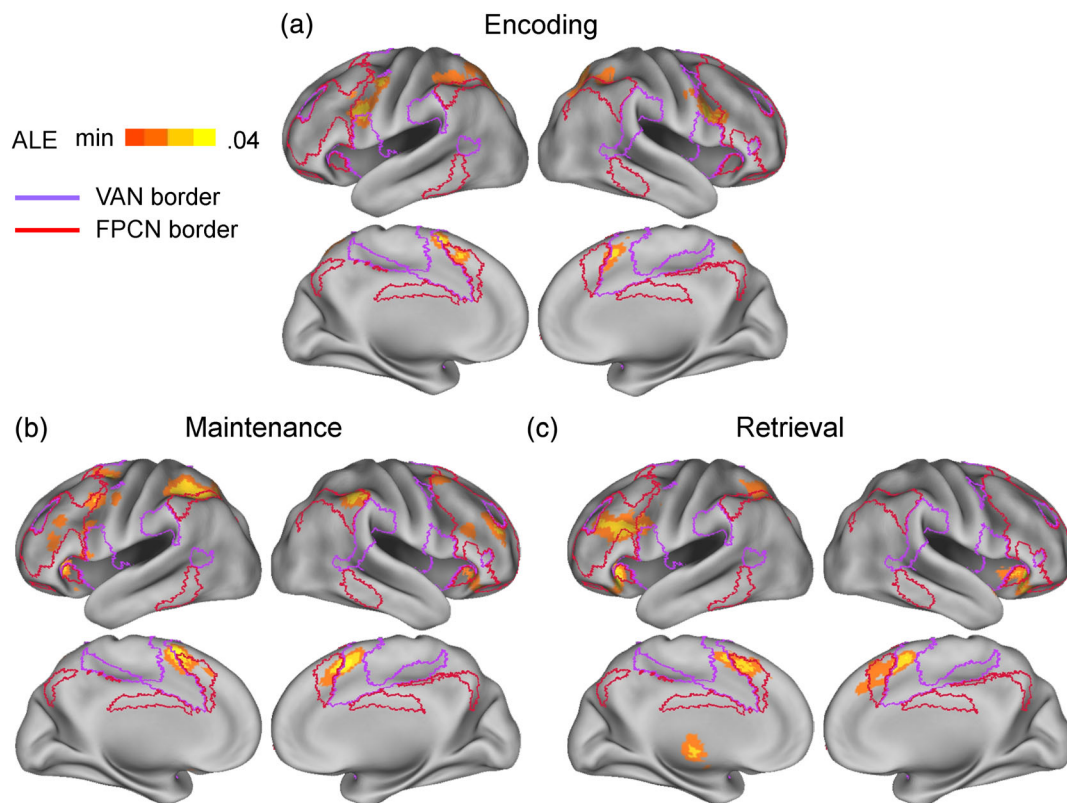


FIGURE 6 Above-threshold regions in separate ALE meta-analyses of (a) encoding-, (b) maintenance-, and (c) retrieval-phase data (the same data shown in Figure 2) are shown with estimated boundaries of the ventral attention network (VAN) and the frontoparietal control network (FPCN) in Yeo et al.'s (2011) 7-network model [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 6 Neurosynth-based image-to-text decoding of encoding-, maintenance-, and retrieval-phase maps

Encoding		Maintenance		Retrieval	
Text	<i>r</i>	Text	<i>r</i>	Text	<i>r</i>
Tasks	.463	Task	.559	Goal	.527
Goal	.445	Working memory	.534	Task	.504
Working memory	.391	Working	.530	Demands	.400
Working	.388	Goal	.524	Working memory	.392
Visual	.326	Load	.414	Working	.388
Load	.314	Demands	.388	Difficulty	.301
Calculation	.288	Memory wm	.362	Load	.297
Attentional	.278	Maintenance	.327	Fear	.258
Demands	.273	Calculation	.319	Task difficulty	.256
Eye	.267	Phonological	.311	Verbal	.240

the FPCN in the phase is consistent with the hypothesis that the network embodies executive function mechanisms (Dosenbach et al., 2008; Niendam et al., 2012; Vincent et al., 2008). Despite its close association with the FPCN, the retrieval phase did not specifically involve its precuneus and mid-cingulate cortex components. On a related note, previous studies showed that long-term memory retrieval recruits these posteromedial regions to a great extent, along with other FPCN regions (for a meta-analysis, see Kim, 2013). Thus, future studies are needed to determine whether recruitment of these regions during long-term, but not WM, retrieval is due to intrinsic differences between memory domains, that is, retrieval of “offline” versus “online” information, or some extrinsic, procedural factors (for related discussion, see Gilmore, Nelson, & McDermott, 2015; Kim, 2018).

The limited involvement of the DAN in the retrieval phase likely reflects multiple factors. First, attention to a probe may be quickly replaced by more persistent attention to internal representations (of the probe and sample stimuli), although such transition likely occurs to some degree in parallel rather than in a strictly serial manner (Bledowski et al., 2006). As discussed earlier, such re-focusing is necessary for efficient memory scanning, decision making, and other controlled processes that are based on internal representations. Second, when a probe is a repeat of a stimulus presented at encoding, repetition suppression effects constrain re-activation of the DAN regions. Indeed, previous studies indicated that many regions within the DAN show repetition suppression to a great extent (for a meta-analysis, see Kim, 2017). Finally, while the memoranda typically consist of multiple items, a probe is in most cases a single item, providing a basis to expect lesser demand on external attention during a retrieval than encoding phase.

4.4 | Comparisons between different phase effects

The current model suggests that the transition from the encoding to maintenance and to retrieval stages involves progressively decreasing recruitment of the DAN, but progressively increasing recruitment of the FPCN. Distributions of regions specific to different phase effects were largely consistent with the model. A subtraction analysis of encoding and maintenance effects indicated that preferential

encoding effects involved two DAN regions, that is, right IFJ and left superior IPS, but no FPCN region, whereas preferential maintenance effects involved many FPCN regions, that is, right mid-lateral PFC, left pmPFC, bilateral anterior insula, and bilateral inferior IPS, but no DAN region. With some minor areas of exception, subtraction analysis between maintenance and retrieval effects and encoding and retrieval effects also indicated similar double dissociations involving the DAN and FPCN that are consistent with the model, although specific within-network sites of dissociations were variable across analyses.

Distributions of regions common to different phase effects were also largely consistent with the model. A conjunction analysis indicates that encoding and maintenance effects commonly involved many DAN regions, that is, left IFJ and left superior IPS/superior parietal lobe, but only one FPCN region, that is, left pmPFC. In contrast, maintenance and retrieval effects commonly involved many FPCN regions, that is, left mid-lateral PFC, bilateral anterior insula, bilateral pmPFC, and left inferior IPS, but only two DAN regions, that is, left IFJ and superior IPS. Only two DAN regions, that is, left IFJ and superior IPS, and one FPCN region, that is, left pmPFC, contributed to both encoding and retrieval phases and to all three phases for that matter. Previous studies showed that the left IFJ contributes to a wide variety of cognitive control tasks, including go/no-go, stop signal, task-switching, Stroop, Posner-cueing, and oddball detection (for meta-analyses, see Derrfuss, Brass, Neumann, & Von Cramon, 2005; Kim, 2014; Levy & Wagner, 2011; Owen et al., 2005), suggesting a more general, cross-functional role than other DAN components. Noting that “the IFJ is located at the junction of three functional neuroanatomical domains, namely the premotor domain, the language domain, and the working memory domain” (p. 316), Brass, Derrfuss, Forstmann, and Cramon (2005) proposed that the region may play an important role in “task representations,” such as representation of stimulus–response mapping rules. Based on this hypothesis, the recruitment of this region in each WM phase may reflect the necessity of maintaining task rules “online” during the whole trial period.

A conjunction analysis between WM-phase maps and Yeo 7 networks also produced results that were largely consistent with the model. Overlap of the phase maps with the DAN progressively decreased from the encoding to maintenance and to retrieval phase,

whereas overlaps with the FPCN increased from the encoding to maintenance phase. However, in an apparent contradiction to the model, the maintenance- and retrieval-phase maps did not appreciably differ in overlaps with the FPCN. While more regions within the frontal components of the FPCN were associated with retrieval than maintenance, the reverse was true for the inferior IPS component of the FPCN (Figure 2b,c), driving relatively equal overlaps with the whole FPCN. A direct, subtraction analysis between maintenance and retrieval effects indicated prominent differences only in the frontal, but not inferior IPS, components of the FPCN (Figure 4b), indicating that any difference involving the inferior IPS component is rather subtle in the magnitude. Taken together, these findings indicate that a greater association of the FPCN with retrieval than maintenance holds for the frontal, but not inferior IPS, components of the FPCN, adding to existing evidence that anterior versus posterior components of the FPCN support differential functions (Brass, Ullsperger, Knoesche, Cramon, & Phillips, 2005; Kim, 2018; Rosen et al., 2016).

A Neurosynth-based decoding showed that WM-phase maps had some commonalities as well as differences in top semantic associates. Common associates included very general task-related terms such as “tasks,” “goal,” and “demands,” and also WM-related terms such as “working memory,” “working,” and “load,” collectively suggesting that WM-related regions serve multiple cognitive, not just WM, demands (Duncan, 2010; Postle, 2006). Specific associates for the encoding map included terms such as “visual,” “attentional,” and “eye” consistent with the hypothesis that WM encoding relies critically on external attention. Those for the maintenance map included terms such as “memory wm,” “maintenance,” and “phonological” suggesting that WM maintenance is typically associated with verbal rehearsal operation (Baddeley, 2012). Those for the retrieval map included terms such as “difficulty,” “task difficulty,” and “verbal” consistent with the hypothesis that WM retrieval demands cognitive control to an extensive extent. Taken together, these results provide valuable information regarding the similarity (and differences thereof) between WM and other cognitive-domain activity maps.

4.5 | Convergence clusters outside the DAN and FPCN

Two cortical clusters, one involving the SMA and the other the frontal operculum, were observed outside the DAN and FPCN. These two clusters were largely within the VAN, contributing to the relatively prominent overlaps of each WM-phase map with the VAN. Two findings indicate that despite their association with the VAN during a resting state, these regions may interact more closely with the FPCN than the VAN during the WM task state. First, most of these effects were co-extensive with adjacent FPCN effects involving the pmPFC and anterior insula. Second, practically no other VAN component, even the posterior core of the VAN known as the temporoparietal junction (Corbetta & Shulman, 2002; Fox et al., 2006; Kim, 2014), specifically contributed to any WM phase. According to Yeo et al. (2011, p. 1138), “the violet ventral attention network is likely an aggregate of (or closely adjacent to) multiple networks in the literature variably

referred to as the salience (Seeley et al., 2007) and cingulo-opercular networks (Dosenbach et al., 2007).” Based on this aggregation and relevant task-based activation and functional connectivity findings (Dosenbach et al., 2007; Gonzalez-Castillo & Bandettini, 2018; Krienen et al., 2014), the anterior insula and pmPFC components of the FPCN likely extend to adjacent frontal operculum and SMA regions during the WM task and also likely during other similar cognitively intensive states.

Two subcortical clusters, one involving the left striatum and the other involving the left thalamus, were observed. First, the left striatum region was associated with the encoding and maintenance phases, but little with the retrieval phase and subtraction analysis indicated a greater association with the encoding or maintenance than retrieval phase. A prominent hypothesis in the WM literature suggests that the striatum subserves gating access to WM or filtering irrelevant information from WM (Geiger et al., 2018; McNab & Klingberg, 2007). The present pattern of results is broadly consistent with this hypothesis in that demand on such gating or filtering function is likely greater during the encoding or maintenance than retrieval phase. Second, the left thalamic region was associated with the retrieval, but not encoding or maintenance, phase. A subtraction analysis indicated a greater association of this region with the retrieval than encoding or maintenance phase, suggesting that it may play an important role in retrieval-related control operations, likely in association with the FPCN. Consistent with this hypothesis, previous functional connectivity studies provided evidence that part of the thalamus is a subcortical module closely associated with the FPCN, perhaps contributing to rapid coordination of control-related signals across the cortex (Beckmann, DeLuca, Devlin, & Smith, 2005; Dosenbach et al., 2007; Halassa & Kastner, 2017).

4.6 | Limitations and conclusions

This study has several limitations, including relatively simplified modeling and hypotheses and the drawbacks of coordinate-based meta-analysis. A more specific limitation is that while the networks provided by Yeo et al.'s (2011) study refer to the “resting state,” the current dataset was obtained during the WM task state. Given that functional coupling across dispersed brain regions differs to some degree between task and rest, despite overall correspondence in network configuration (Buckner et al., 2013; Krienen et al., 2014), Yeo et al.'s 7-network model can only provide an approximate, but not exact, framework for interpreting the current results. Another limitation is that some results may be related more to the specifics of widely employed procedures, such as the use of perceptually simple stimuli and the requirement of decision making during a retrieval, but not other, phase, than to the intrinsic properties of WM.

Evidence from electroencephalography (EEG) and magnetoencephalography (MEG) studies show that the nature of the information representation in a brain region can dynamically change in the order of milliseconds, posing an inferential challenge for studies using low temporal resolution measures such as fMRI (Ghuman & Martin, 2019). Using a Sternberg-type WM task and complex source reconstruction

algorithm, an MEG study (Heinrichs-Graham & Wilson, 2015) indicated that occipital areas showed alpha/beta desynchronizations beginning immediately after the onset of encoding stimuli, which became gradually weaker as a function of time during encoding and eventually evolved into a strong synchronization during the late maintenance period. In contrast, similar desynchronizations in the left dorsolateral PFC and superior temporal areas became progressively stronger as a function of time during encoding and were sustained during most of the maintenance period until being sharply dispelled just before retrieval. This and other related EEG/MEG findings (e.g., Brookes et al., 2011; Palva, Kulashekhar, Hämäläinen, & Palva, 2011; Pinal, Zurrón, & Díaz, 2014) indicate that WM-related activity observed in fMRI studies is mix of dynamic changes on the level of milliseconds, warranting its cautious interpretation. A multi-modal approach that combines fMRI and EEG/MEG has great potential to enhance our understanding of within-phase activity changes during WM tasks.

Within the limitations described above, the present study reveals the dynamic unfolding of intrinsic network participation in WM temporal subprocesses. In particular, the proposed model essentially suggests that the transition from the encoding to maintenance and to retrieval stages involves progressively decreasing involvement of the DAN, but progressively increasing involvement of the FPCN. Separate meta-analysis of each phase effect and direct comparisons between them yielded results that were largely consistent with the model. Pairwise contrasts between different phase effects indicated double dissociations involving the DAN and FPCN, thereby providing the strongest supporting evidence for the model. Two closely juxtaposed regions that are members of the DAN and FPCN, such as IFJ versus caudal PFC and superior versus inferior IPS, showed a high degree of functional differentiation. In conclusion, although all regions identified in the present study were already identified in previous WM studies, this study uniquely enhances our understating of their roles by clarifying their network membership and specific associations with different WM phases.

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CONFLICT OF INTEREST

The author declares that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in NeuroVault at <https://identifiers.org/neurovault.collection:5506>.

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