

# Portraying the unique contribution of the default mode network to internally driven mnemonic processes

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Numerous neuroimaging studies have implicated default mode network (DMN) involvement in both internally driven processes and memory. Nevertheless, it is unclear whether memory operations reflect a particular case of internally driven processing or alternatively involve the DMN in a distinct manner, possibly depending on memory type. This question is critical for refining neurocognitive memory theorem in the context of other endogenous processes and elucidating the functional significance of this key network. We used functional MRI to examine DMN activity and connectivity patterns while participants overtly generated words according to nonmnemonic (phonemic) or mnemonic (semantic or episodic) cues. Overall, mnemonic word fluency was found to elicit greater DMN activity and stronger within-network functional connectivity compared with nonmnemonic fluency. Furthermore, two levels of functional organization of memory retrieval were shown. First, across both mnemonic tasks, activity was greater mainly in the posterior cingulate cortex, implying selective contribution to generic aspects of memory beyond its general involvement in endogenous processes. Second, parts of the DMN showed distinct selectivity for each of the mnemonic conditions; greater recruitment of the anterior prefrontal cortex, retrosplenial cortex, and hippocampi and elevated connectivity between anterior and posterior medial DMN nodes characterized the semantic condition, whereas increased recruitment of posterior DMN components and elevated connectivity between them characterized the episodic condition. This finding emphasizes the involvement of DMN elements in discrete aspects of memory retrieval. Altogether, our results show a specific contribution of the DMN to memory processes, corresponding to the specific type of memory retrieval.

free recall | memory search | word fluency

The default mode network (DMN) is known to play a central role in internally based processes, including self-referential operations (1–4), internal mentation (5), and unconstrained thinking (6, 7). Additionally, during the past decades, the DMN has consistently been implicated in both semantic (8, 9) and episodic (10–13) memory processes. However, despite the fact that internal operations are inherent to many, if not all, mnemonic tasks, the unique contributions of the DMN to memory operations beyond its more general role in nonmnemonic internally based processes have not been sufficiently addressed thus far.

One example of an internally based mnemonic process is mental search, which plays a central role in memory retrieval (14). Although a significant contribution of the DMN to memory search has been shown (12, 15), it is yet unclear whether this contribution merely reflects the DMN's involvement in non-specific internal direction of attention or rather, a specific role for the DMN in mnemonic search processes. Direct comparison of DMN recruitment during memory search with its recruitment during nonmnemonic internal search operations may shed light on this matter.

This question can be further broken down into the contribution of DMN subcomponents to various mnemonic processes. The

neural commonalities and differences of nonautobiographic (e.g., laboratory) and autobiographic episodic memory and semantic memory were recently examined, revealing a common functional network that included the inferior frontal gyrus (IFG), the middle frontal gyrus, the caudate nucleus, the thalamus, the lingual gyrus, and the left hippocampus (16). Interestingly, although these regions do not belong to the core DMN, some of them were functionally connected with DMN components during the performance of the various memory tasks (17). In a recent meta-analysis of semantic memory, the similarities between the recruitment patterns obtained in the DMN and those patterns that are typical to autobiographic episodic memory were noted (8). Nevertheless, to the best of our knowledge, a direct comparison of semantic and episodic memory, focused on the contribution of the DMN to each memory type, has not yet been performed. Characterization of the similarities and dissimilarities of DMN activation patterns in episodic and semantic memory is anticipated to shed light on the relations between episodic and semantic memory, a controversial issue that has attracted much investigational interest and effort over the years (18, 19).

The present study aims are, thus, twofold. First, to elucidate the unique contribution of the DMN to internally generated aspects of mnemonic processes as opposed to nonmnemonic ones. Second, to characterize and compare the DMN recruitment patterns selectively associated with two major types of mnemonic operation: semantic and episodic. To accomplish these aims, we examined the DMN activity and connectivity patterns that occur during word fluency tasks that are known to maximize the reliance on internal search processes and thus, probably involve recruitment of the DMN. To test the unique contribution of the DMN with regard to mnemonic memory search, we compared mnemonic (episodic and semantic) word fluency with nonmnemonic phonemic (letter) word fluency. To test the recruitment with regard to specific memory types, we compared episodic and semantic word fluency. Specifically, we used word fluency based on free recall of words from previously shown lists, which is traditionally considered to reflect episodic memory capabilities, and word fluency based on generation of words belonging to a particular category, which is traditionally considered to reflect semantic memory (20). Notably, the three experimental conditions share many features, including joint use of search strategies, such as initiation and direction, and control processes, such as verification and monitoring. The main difference is in the selection criteria defined as an episodic memory tag, semantic memory feature, or nonmnemonic phonological attribute. Each selection criterion leads to the application of different internal search operations. We hypothesized that mnemonic word

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fluency would involve greater recruitment of the DMN compared with nonmnemonic word fluency. In view of recent indications of functional heterogeneity of the DMN, reflected in different levels of recruitment of its distinct nodes during mnemonic tasks (15), we further hypothesized that distinct DMN components would contribute in different ways to the semantic and episodic word fluency tasks.

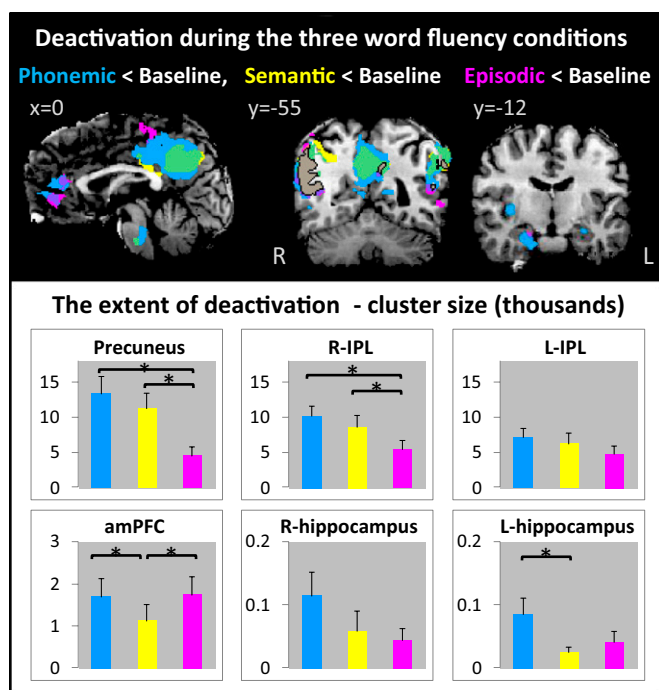
## Results

**Recruitment of the DMN During Word Fluency Conditions.** Changes in DMN activity during each of the word fluency conditions were identified by contrasts with baseline fixation as a basic model for whole-brain analysis (condition < baseline) (2, 5, 21, 22). Five major results were obtained from this analysis (Fig. 1, *SI Materials and Methods*, and *Table S1*). First, as expected, the various nodes of the DMN were deactivated during the three word fluency tasks compared with baseline. Second, across all three conditions, the right inferior parietal lobule (IPL) was more deactivated compared with the left IPL [ $F_{(1,15)} = 7.62, P < 0.02$ ], reflecting the verbal nature of the tasks and language organization in the human brain. Third, deactivation was found to be more dispersed during phonemic fluency compared with the two mnemonic word fluency conditions (Fig. 1, posthoc comparisons). Fourth, the anterior medial prefrontal cortex (amPFC) was more deactivated during the phonemic and episodic conditions than the semantic condition, signifying more involvement of this region in semantic retrieval [ $F_{(2,30)} = 5.01, P < 0.02$ ]. A similar pattern was observed

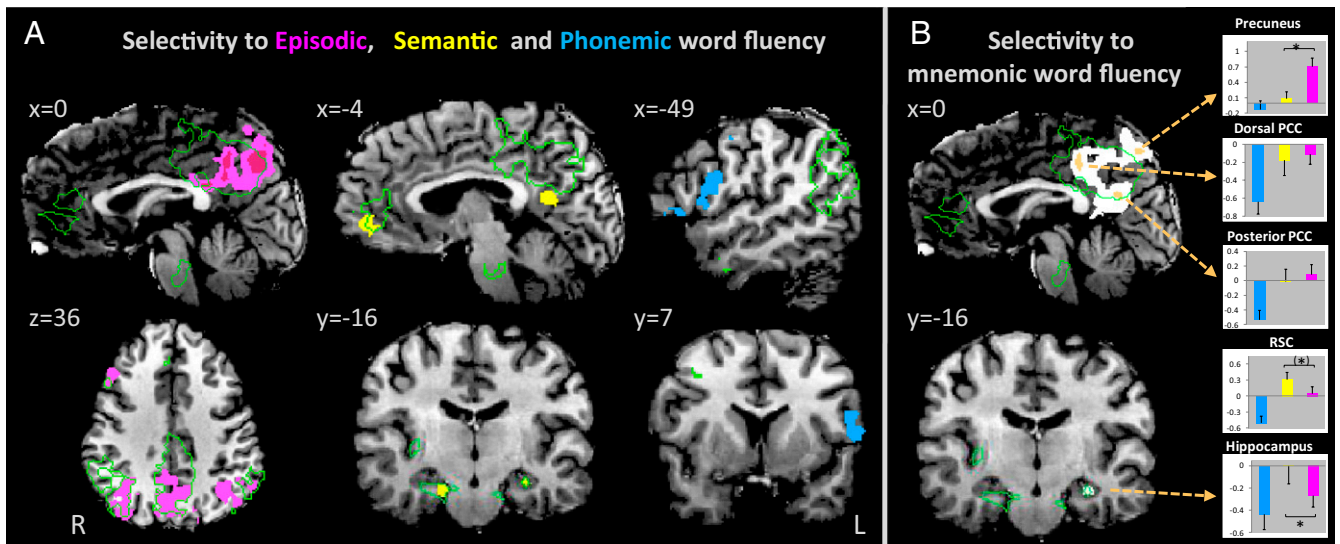
in the left hippocampus, with diminished deactivation in the semantic compared with the phonemic condition [ $F_{(2,30)} = 4.53, P < 0.02$ ]. Fifth, distributed and extensive deactivation was seen in the precuneus [ $F_{(2,30)} = 16.00, P < 0.01$ ] and right IPL [ $F_{(2,30)} = 9.11, P < 0.01$ ] during semantic and phonemic word fluency, whereas only limited deactivations were seen during episodic word fluency, implying that posterior nodes of the DMN play a unique role in episodic fluency. Notably, these relative deactivations do not necessarily represent a direct contribution of each region to each of the tasks. It is possible that the degree of deactivation reflects an indirect contribution (that is, inhibitory modulation by other task-related regions on DMN regions).

**Selectivity to Each of the Word Fluency Conditions.** To identify brain regions that uniquely contribute to each of the word fluency conditions, each condition was directly compared with the two other conditions. Whole-brain analysis showed selectivity to semantic word fluency in the amPFC, retrosplenial cortex (RSC), left superior frontal gyrus (SFG), bilateral hippocampi, and parahippocampus (Fig. 2A, yellow and *Table S2*). Several of these selective regions correspond to regions deactivated during the task (that is, to the DMN) (Fig. 2A, outlined in green). Selectivity to episodic word fluency was seen in the posterior cingulate gyrus (PCC), precuneus, IPL, bilateral intraparietal sulcus (IPS), bilateral SFG, and right anterior lateral PFC (Fig. 2A, pink and *Table S2*). Thus, selectivity to the episodic condition was seen mainly in posterior nodes of the DMN (Fig. 2A, outlined in green), extending caudally and dorsally to non-DMN parts of the posterior parietal cortex. Selectivity to phonemic word fluency was evident in the left dorsal premotor cortex and left IFG as well as in left IPS (Fig. 2A, blue and *Table S2*). The opposite contrast revealed brain regions that reduce activity in the phonemic condition compared with the mnemonic ones, including the PCC, left hippocampus, and bilateral parahippocampus (Fig. 2B, white and *Table S2*). Notably, similar selectivity patterns were seen in a conjunction analysis, requiring regions to increase activation during the condition of interest, compared with each of the two other conditions (Fig. S1); although some results of the conjunction analysis did not survive false discovery rate (FDR) correction, they were robust to cluster-level threshold correction for multiple comparisons ( $\alpha < 0.05$ ) (details in Fig. S1). The main difference is a lack of selectivity to mnemonic processes in the hippocampus (Fig. S1B), implying a selective contribution to semantic word fluency rather than a generic contribution to mnemonic processes. Several regions were elicited as both mnemonic-generic and task-specific. To further clarify their role, the semantic and episodic conditions were directly compared within these regions (Fig. 2B, bar plots and *SI Results*), revealing significant differences in the hippocampus [ $t_{(15)} = 2.36, P < 0.03$ ] and precuneus [ $t_{(15)} = -5.85, P < 0.01$ ] and a trend in RSC [ $t_{(15)} = 2.07, P < 0.056$ ] but no differences in the dorsal [ $t_{(15)} = -0.62, P < 0.55$ ] and posterior [ $t_{(15)} = -0.57, P < 0.58$ ] PCC. These findings indicate a generic contribution of PCC components to mnemonic processes and task-specific contributions of the hippocampus, RSC, and precuneus.

**Sensitivity to Task Performance.** To identify brain regions that uniquely contribute to performance on each of the word fluency conditions, the parametric predictor representing the number of responses in each repetition time (TR) of each condition was directly compared with the parametric predictors of the two other conditions. Direct comparisons were conducted within brain regions that selectively contribute to each of the word fluency conditions (the two highest peaks in each network were examined) (*SI Results*). A selective semantic parametric effect was seen in the RSC [ $t_{(15)} = 2.84, P < 0.01$ ], with a similar trend seen in the left parahippocampus [ $t_{(15)} = 1.73, P < 0.10$ ]. Selective phonemic parametric effects were seen in the left premotor cortex



**Fig. 1.** Recruitment of the DMN during the word fluency tasks. Whole-brain group activation maps of regions showing deactivation during the phonemic (blue), semantic (yellow), and episodic (pink) word fluency tasks compared with baseline fixation. Overlaps between the phonemic and semantic conditions are presented in green, overlaps between phonemic and episodic conditions are presented in purple, and overlaps between the three conditions are presented in gray (with black outline). Random,  $n = 16, P < 0.05$  FDR-corrected, cluster size  $> 5 \times 3^3$  voxels. Cluster size (in thousands of voxels) is presented in six key regions. The amPFC and left hippocampus were less deactivated during semantic word fluency, whereas posterior DMN nodes (right IPL and precuneus) were less deactivated during episodic word fluency. \*Significant differences in cluster size between the word fluency conditions (Tukey posthoc comparisons,  $P < 0.05$ ).



**Fig. 2.** Selectivity to the word fluency tasks. (A) Whole-brain group activation maps of regions showing increased activity during the phonemic (blue), semantic (yellow), and episodic (pink) word fluency tasks. Each condition was compared with the other two conditions. The green outline marks the regions that were deactivated during any of the tasks (that is, the DMN). Selectivity to the episodic and semantic word fluency tasks includes DMN components, whereas selectivity to the phonemic word fluency condition is seen in classic language areas. Random,  $n = 16$ ,  $P < 0.05$  FDR-corrected, cluster size  $> 5 \times 3^3$  voxels. (B) Whole-brain group activation maps of regions showing greater response during the mnemonic conditions (semantic and episodic word fluency) compared with the nonmnemonic condition (phonemic word fluency). Greater recruitment of the posterior cingulate nodes of the DMN was seen during mnemonic word fluency. The RSC is lateralized and not shown in the midsagittal section. Random,  $n = 16$ ,  $P < 0.05$  FDR-corrected, cluster size  $> 5 \times 3^3$  voxels. The bar plots present the averaged  $\beta$ -values in mnemonic-selective regions (marked in orange).

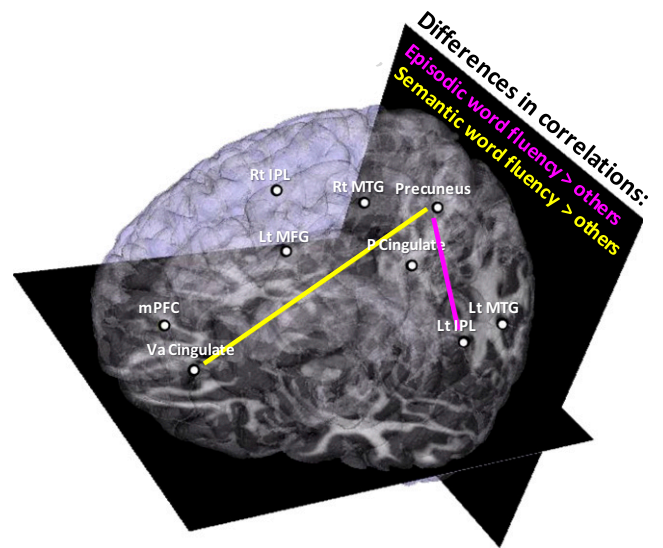
$[t_{(15)} = -2.96, P < 0.01]$  but not the left IFG  $[t_{(15)} = -1.24, P < 0.24]$ . A trend for selective episodic parametric effects was seen in the anterior aspect of the precuneus  $[t_{(15)} = -2.02, P < 0.06]$  but not the posterior  $[t_{(15)} = 0.238, P < 0.79]$ . Selective mnemonic parametric effects were not obtained in the dorsal  $[t_{(15)} = 0.29, P < 0.77]$  or the posterior PCC  $[t_{(15)} = 0.29, P < 0.77]$ .

**Interregional Functional Connectivity.** We next examined whether functional connectivity between pairs of DMN nodes differed in the two mnemonic word fluency conditions (*SI Materials and Methods*). This analysis indicated greater correlations between the anterior and posterior medial components of the DMN in the semantic condition compared with the other conditions (Fig. 3, yellow)  $[t = 4.84$  for the connection between the precuneus and ventral anterior cingulate]. Greater connectivity within posterior DMN components was seen in the episodic condition compared with the other conditions  $[t = 6.22$  for the connection between the precuneus and left IPL] (Fig. 3, pink).

**Discussion**

Several findings from the present study point to a unique role of the DMN in memory beyond its general contribution to internally driven search processes. Indeed, a large portion of the regions uniquely recruited during episodic and/or semantic word fluency, but not phonemic fluency, are, in fact, included in what is known as the DMN (Fig. 24). In several of these regions, activity is selectively related to search successes, further corroborating their unique contribution to the task at hand. In addition, deactivations in the DMN were generally less evident during mnemonic than nonmnemonic word fluency (Fig. 1). Finally, components of the DMN were found to be more interconnected during mnemonic compared with nonmnemonic word fluency tasks (Fig. 3). Taken alone, these results affirm a distinctive role of the DMN in memory operations. Nevertheless, the design of this study enabled the demonstration of significant differences between DMN subcomponents with regard to their involvement in the two mnemonic conditions. Specifically, only

in the PCC did both types of mnemonic word fluency similarly elicit less deactivation than the nonmnemonic condition (Fig. 2B, bar plots), implying a generically selective role for this region in memory beyond its overall involvement in endogenous processes. In other DMN regions, such as the precuneus, IPL, and amPFC, only one of the mnemonic word fluency tasks was accompanied by a unique activity or connectivity pattern, whereas the other resembled the nonmnemonic task (Figs. 1, bar plots, 24, and 3),



**Fig. 3.** Functional connectivity within the DMN. Significant differences between the degree of correlation of each pair of DMN nodes in the three word fluency conditions ( $P < 0.05$ , Bonferroni-corrected). Posterior parts of the DMN are more interconnected during episodic memory compared with other word fluency conditions, whereas the anterior aspect of the DMN is more connected to posterior aspects of the DMN in the semantic condition compared with other word fluency conditions.

indicating involvement in specific aspects of mnemonic retrieval rather than a generic role in memory processing.

**Generic Role of the PCC in Retrieval of Memories.** We found that PCC activation differentiated between mnemonic and nonmnemonic word fluency, strongly supporting its role in retrieval processes (Fig. 2B). The PCC has been indicated as an integral part of the Papez circuit that plays an important role in memory processes (23). A key property of both semantic and episodic memory is the integration of various modalities, behaviors, and functions during both encoding and retrieval: the formation of memories requires integration of external information received through various sensory modalities as well as internally generated information; the access to and expression of stored memories is highly flexible, conducted through multiple routes, and observed in a range of behaviors. Both mnemonic processes interact closely with other cognitive and affective functions (24). In addition, both semantic and episodic memories are continuously acquired, a unique quality supposedly manifested by a persistently high metabolic activity. The structural and functional characteristics of the PCC lead us to hypothesize that this region may mediate the flexible multimodal access to and multibehavioral expression of amalgamated memories. The suggestion for this integrative role derives from the classification of the PCC as a major cortical hub (25, 26), its high metabolic rate (27), its massive connectivity with widespread brain regions (26), particularly with the hippocampus (28), its established contribution to semantic (8) and episodic (11, 29) memory, and most importantly, its crucial role in memory processing made evident in lesion studies (30, 31). Notably, this proposition corresponds with the recently suggested role of the PCC in monitoring and flexibly reacting to environmental changes through continuous integration of internal and external information as well as cognitive and motor behaviors (26, 32).

**Contributions of DMN Subcomponents to Specific Aspects of Memory.** In line with recent evidence of the functional heterogeneity of the DMN (3, 4, 6, 15, 33–35), various parts of the DMN showed differential activation and connectivity patterns during the two mnemonic word fluency tasks. Direct contrasts of the word fluency conditions revealed discrete recruitments of DMN for each retrieval type: anterior PFC, RSC, and hippocampal components during the semantic task in contrast to mainly posterior DMN components during the episodic task (Fig. 2A). In view of the highly heterogeneous nature of the PCC (26, 36), the fact that some regions play a generic role in memory, whereas a subregion in the RSC is selective for semantic word fluency, is not surprising. Similarly, interregional connectivity analyses yielded distinguished connectivity patterns during the two mnemonic conditions: elevated coactivation between the precuneus and ventral anterior cingulate during the semantic condition and between the precuneus and the left IPL during the episodic condition (Fig. 3). Although the definitions of semantic and episodic memory in this manuscript conform to the traditional distinction of semantic and episodic memory types, the interdependency between these memory types has been widely acknowledged (18, 24, 37–39). Thus, task-specific activity/connectivity patterns are interpreted below through emphasis of the type of information being retrieved in each memory task (19, 40) rather than a semantic–episodic dichotomy. Accordingly, the specific role of a distinct region can be elucidated by considering the specific type of information retrieved during the task along with what is known from the literature regarding its nonmnemonic roles. These assignments were guided by the well-accepted principle of reinstatement, according to which retrieval of memories activates the same neural ensembles underpinning sensation and perception during the original event (i.e., during memory formation) (41–43).

The finding of selective episodic memory activation (Fig. 2) and elevated coactivation (Fig. 3) in the parietal lobe corroborates previous evidence of the functional significance of the lateral (44, 45) and medial (30, 31) aspects of the posterior parietal cortex in episodic memory retrieval, particularly within the precuneus, IPL, and IPS (15, 19, 46–48). The results of the present study point to the posterior parietal cortex as the key region differentiating laboratory episodic tasks more successfully than structures typically associated with episodic memory. Our episodic task required the retrieval of recently tagged words while distinguishing words that were tagged during the practice and scan sessions. Unlike the two other conditions, the episodic task necessitated the retrieval of precise spatial (task location: room/scanner) and/or temporal (task timing: before/during scan) information related to the searched words. In view of the recognized role of the precuneus and IPS in processing spatial (40, 49, 50) and temporal (51) information, possibly through a single parietal magnitude system (52), the present finding allows us to further suggest that these regions are involved in the representation of temporal–spatial aspects of memories. Indeed, increased recruitment of the precuneus was seen during the retrieval of spatially detailed memories (53).

Numerous studies show the critical role of hippocampi in memory (54, 55). Remarkably and unexpectedly, not only were the hippocampi not selectively activated during the episodic task, they were found to be more activated by the semantic task (Fig. 2A). Over the past decades, the idea that the hippocampi exclusively support episodic as opposed to semantic memory has been challenged (56), and the contribution of the medial temporal lobe in semantic fluency tasks has gradually become acknowledged (57). The pattern of greater activation during the semantic task is consistent with a recent report of hippocampus suppression during laboratory episodic memory search in humans (58). Hippocampus involvement in the semantic word fluency task can be explained by the type of information retrieved in our study. Specifically, reliance on autobiographical contextual information as a retrieval strategy during semantic word fluency tasks has been previously shown (19, 57, 59) and may contribute to the greater recruitment of the hippocampi seen in the present study during the semantic condition (8, 11).

In addition to the hippocampi, greater recruitment was also found within the medial PFC and the RSC during the semantic condition. The joint recruitment of bilateral hippocampi and RSC during semantic fluency is consistent with the similar activity patterns seen in these structures in a different memory task (60). The involvement of hippocampi and RSC in semantic word fluency may further explain the degraded performance of individuals with Alzheimer's disease on semantic fluency tasks (61), because the earliest metabolic decline in Alzheimer's disease is centered on the RSC (62, 63), whereas early structural changes are seen in the hippocampi (63).

Notably, the episodic and semantic tasks also differ in terms of the age of the memory: although the retrieved semantic and phonemic knowledge has been acquired over many years, the episodic tagging occurred within a time frame of minutes. It has been claimed that the neural representation of memories dynamically changes with time and rehearsal. For example, the binding process of various components of semantic (64) and possibly, also episodic (65) memories is transferred from the medial temporal lobe (MTL) to the neocortex. Nevertheless, in the present study, greater hippocampus activation was evident in the semantic rather than the episodic condition. An alternative explanation could be that hippocampi recruitment represents novelty-encoding differences; the items in the episodic condition were already associated with the experimental context, whereas items retrieved from semantic memory are contextually novel. Nevertheless, the lack of comparable hippocampi recruitment during the phonemic task rules out this interpretation. However, the novelty of memories could have

affected the dissociation between the two memory types in the current study. While retrieval of the long-term consolidated knowledge is irrelevant and nonbeneficial in the episodic and phonemic conditions, it is necessary in the semantic condition. Animal (66) and human (67, 68) studies implicate the mPFC in remote memory, possibly underlying the greater recruitment of this region during the retrieval of more distant semantic memories. Similar to the semantic/episodic dissociation observed in the present study, conjoint recruitment of the hippocampi, RSC, and mPFC was also evident in a human imaging study during incidental retrieval of long-term preexperimental knowledge, whereas the precuneus was recruited during the retrieval of task-related recent information (69). The present results extend this finding, suggesting that the hippocampus–RSC–mPFC circuit is also involved in intentional retrieval of task-relevant long-term knowledge.

In conclusion, the present study shows that DMN does not show a unified involvement in memory processes. Although an eminent DMN component has been found to exert mutual activation patterns across memory types, other key DMN regions are involved in memory in an attuned way to the specific type of memory or type of information at hand. We suggest that the frequently seen recruitment of the entire DMN during memory tasks may reflect the fact that rich coherent memories usually encompass multiple types of information. A delicate balance within the DMN may forge a memory by optimizing the internal search and retrieval of specific mnemonic aspects.

## Materials and Methods

**Procedure.** Eighteen participants performed a word fluency paradigm consisting of three conditions: phonemic fluency, during which participants generated words that began with a given letter; semantic fluency, during which participants generated exemplars from a given semantic category; and episodic fluency, during which participants generated words from previously studied word lists (that is, freely recalled words that were studied earlier). In all tasks, participants were instructed to generate as many words as possible, with specific stimuli chosen to prevent ceiling effects. Each of the three word fluency conditions (phonemic fluency, semantic fluency, and episodic fluency) was performed six to eight times in an 18-s block separated by visual fixation. Participants' overt verbal responses were recorded and analyzed offline (details in *SI Materials and Methods*).

**Functional MRI Data Acquisition and Analyses.** Imaging was performed with a 3.0T MRI scanner (GE Signa EXCITE) using an eight-channel head coil. Functional

T2\*-weighted images were obtained using field of view = 200 mm, matrix size = 96 × 96, repetition time = 3,000 ms, echo time = 35 ms, flip angle = 90°, 39 axial slices of 3-mm thickness, and gap = 0. To eliminate potential confounders associated with task difficulty and articulation effects, performance in the three word fluency conditions was controlled at the individual participant level, such that the difference between the average of each fluency condition did not exceed two words. Details regarding pre- and postbalanced performance are in *SI Results*.

Functional MRI data were analyzed with the BrainVoyager analysis package (version 2.1; Brain Innovation). After a standard preprocessing (*SI Materials and Methods*), an individual protocol was prepared for each participant, including a TR-based parametric regressor for each condition constructed based on his/her performance, weighting each TR unit according to the number of words generated in that TR. Participants' general linear models defined seven regressors: three predictors uniformly representing the balanced phonemic, semantic, and episodic blocks; three predictors parametrically representing the balanced phonemic, semantic, and episodic blocks; and the do not care predictor with the unbalanced blocks. The weights of parametric predictors were Z-transformed and orthogonalized with respect to the main effect predictors. All regressors were modeled as boxcar functions convolved with the hemodynamic response function. Notably, despite overt responding, head movements did not exceed 2 mm/degree. Single-subject analysis was followed by a multisubject analysis computed with random effects using a gray matter mask. In all analyses, brain activations were assessed at a statistical threshold of  $P < 0.05$  using FDR correction for multiple comparisons and a minimal cluster size of  $5 \times 3^3$  voxels (*SI Materials and Methods*).

**Interregional Functional Connectivity Analysis.** To analyze the dynamics of the functional connectivity within the DMN, we first defined regions of interests (ROIs) using a Gaussian mask with a 4-mm radius around the peaks of activation reported in a metaanalysis of the DMN (34). The signal was extracted from all ROIs, and a set of all pairwise Pearson correlation values were calculated for each subject and condition, incorporating a hemodynamic delay of 2 TRs. After a Fisher Z transformation, two-tailed  $t$  statistics were computed to compare conditions. All pairwise ROIs with connections that were significant at the  $P < 0.00069$  level (i.e.,  $\alpha < 0.05$  threshold with Bonferroni correction) are connected (*SI Materials and Methods*).

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