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Coactivation of the Default Mode Network regions and Working Memory Network regions during task preparation

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The Default Mode Network (DMN) regions exhibit deactivation during a wide variety of resource demanding tasks. However, recent brain imaging studies reported that they also show activation during various cognitive activities. In addition, studies have found a negative correlation between the DMN and the working memory network (WMN). Here, we investigated activity in the DMN and WMN regions during preparation and execution phases of a verbal working memory task. Results showed that the core DMN regions, including the medial prefrontal cortex and posterior cingulate cortex, and WMN regions were activated during preparation. During execution, however, the WMN regions were activated but the DMN regions were deactivated. The results suggest that activation of these network regions is affected by allocation of attentional resources to the task relevant regions due to task demands. This study extends our previous results by showing that the core DMN regions exhibit activation during task preparation and deactivation during task execution.

Recent brain imaging studies showed that there are a number of large-scale brain networks, resting state and task-related, including the dorsal attentional network (DAN), the frontoparietal network (FPN) or executive working memory network (WMN), the primary motor network, the primary visual network, and the Default Mode Network (DMN)^{1–7}. These networks may sometimes work together to perform tasks, but may compete with each other for processing resources.

The DMN typically consists of the medial prefrontal cortex (MPFC), the posterior cingulate (PCC)/precuneus, inferior parietal lobe (IPL), lateral temporal cortex (LTC), and hippocampal formation (HF)^{8,9}. Core regions of the DMN include MPFC and PCC. The DMN was originally discovered as a network of regions that showed deactivation during some goal-directed cognitive tasks compared to a resting baseline^{8,10–16}. However, recent studies have reported that the DMN shows activation during a wide range of cognitive tasks, including stimulus independent thought^{11,14}, mind wandering^{17,18}, monitoring of the external environment^{15,18}, self-reference¹¹, autobiographical and prospective memory^{19,20}, and social cognition^{21,22}.

Deactivation in the DMN might be related to Task Induced Deactivation (TID), which is task induced allocation of attentional resources due to processing demands. Previous studies showed that attention affects activity in the task-positive brain regions^{13,23–27}. Shmuel et al.²⁸ found that the negative BOLD response outside the stimulated regions was associated with decreases in neuronal activity below spontaneous baseline activity. According to this view, deactivation in the DMN reflects allocation of cerebral resources in order to support task performance^{14,29}, and some studies suggested that dynamic suppression of the DMN regions is necessary for accurate behavioural performance on cognitively demanding tasks^{30–32}. Buckner et al.³³ suggested that the DMN and the external attention system are competing with each other. The DMN tends to reduce activation when attention is focused on a particular task, whereas the DMN tends to increase activation when attention is rather relaxed.

Previous studies reported supporting data for this view. Negative correlations have been found between the DMN and other brain regions including the WMN, such that the higher the activation in the WMN, the lower the activation in the DMN^{8,32,34–39}. Furthermore, the level of activation and deactivation seem to be related to task demands and task performance. Mayer et al.⁴⁰ reported that the DMN showed greater deactivation when the task difficulty was higher. Chadick and Gazzaley⁴¹ reported that visual areas that selectively process relevant information are functionally connected with the FPN, whereas the areas that process irrelevant information are coupled



with the DMN. They claimed that sensory areas are differentially and dynamically coupled with different networks depending on task goals.

Recent studies, however, showed that DMN and WMN may not always be negatively correlated. The DMN may be coactive and functionally coupled with the WMN in some tasks including planning for personal future²², mental simulations⁴², evaluation of creative work⁴³, social working memory⁴⁴, and scene construction⁴⁵. Furthermore, Anticevic et al.⁴⁶ reported that the temporoparietal junction (TPJ) and DMN were both deactivated during an encoding phase of a WM task, whereas they were functionally decoupled during a successive distractor processing phase. They concluded that TPJ and DMN may collaborate with each other depending on task demands. In our previous study, we also found that the anterior MPFC, a part of the DMN, was activated during preparation of a working memory task⁴⁷, but was deactivated during execution of the task, suggesting that activation and deactivation of MPFC might be influenced by allocation of attentional resources due to task demands. Taken together, these studies suggest that the DMN and WMN regions may be coactive during task preparation; however, during task execution, the WMN remains active whereas the DMN might be deactivated.

We investigated this possibility in the present study using a dual task procedure. A primary task was a verbal WM task, and a background task was simple addition of four single-digits presented successively one at a time at the centre of the screen. In the WM task, participants saw four words on the screen. We set up three experimental conditions. One is a Category judgment condition, in which participants were asked to find an odd item among the four words. At the end of the trial, a probe word was presented, and the participants were asked to judge whether or not the probe word was an odd item. Another is a Memory condition, in which they were required to remember the words. At the end of the trial, they were required to judge whether or not the probe word was among the four words previously presented. These two conditions were dual task conditions and they performed addition together with the WM task. The third is a single task condition, in which they ignored the words and performed addition only. They were asked to determine the number of letters in the probe word when it was introduced. As was our previous study, there were two phases in each trial: a preparation period, in which participants were asked to prepare for the trial by forming a task set, and an execution period, in which they performed the task. An example of trial sequence is shown in Figure 1. The participants also performed the Japanese version of the Reading

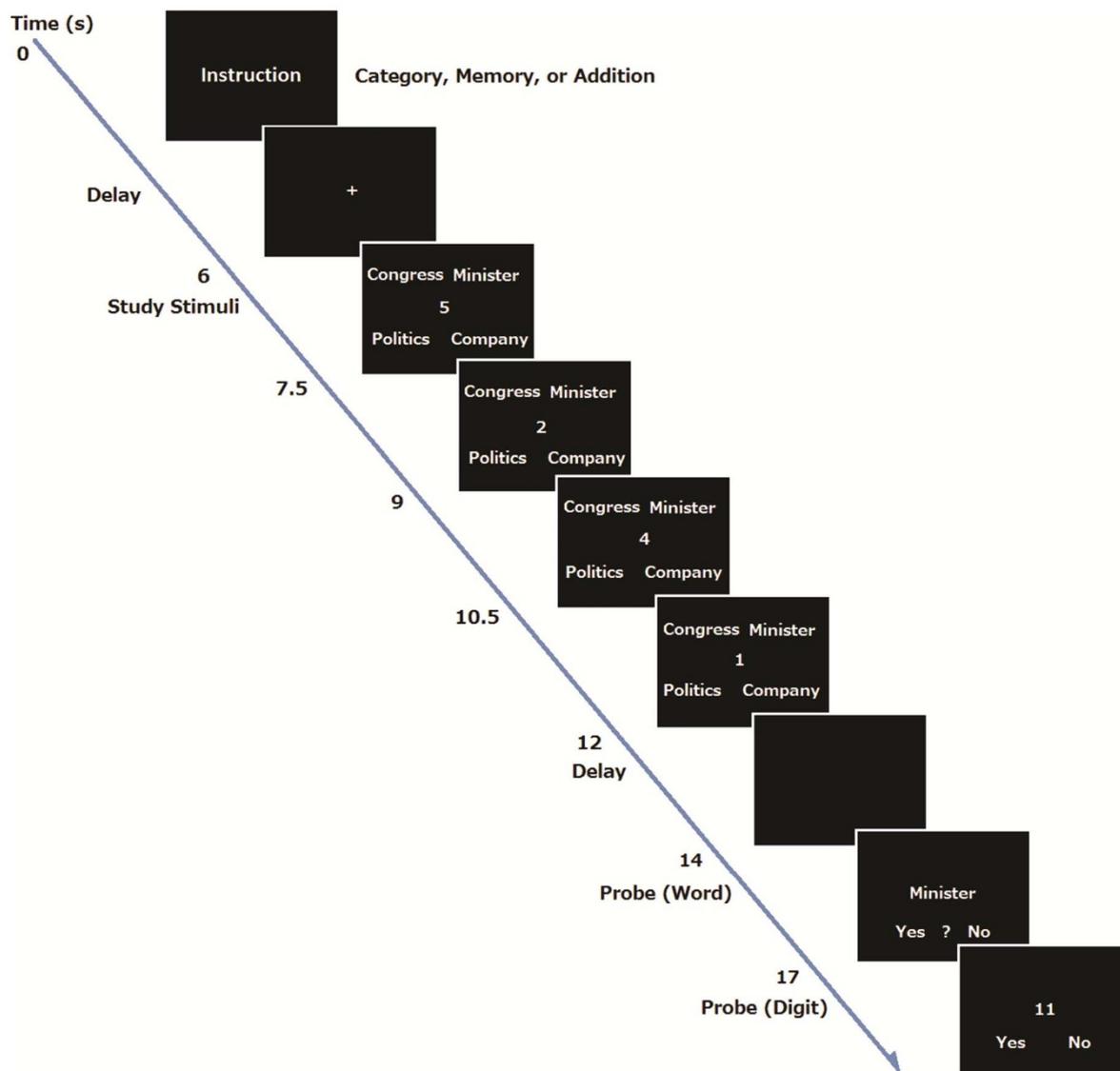


Figure 1 | An example of trial sequence.

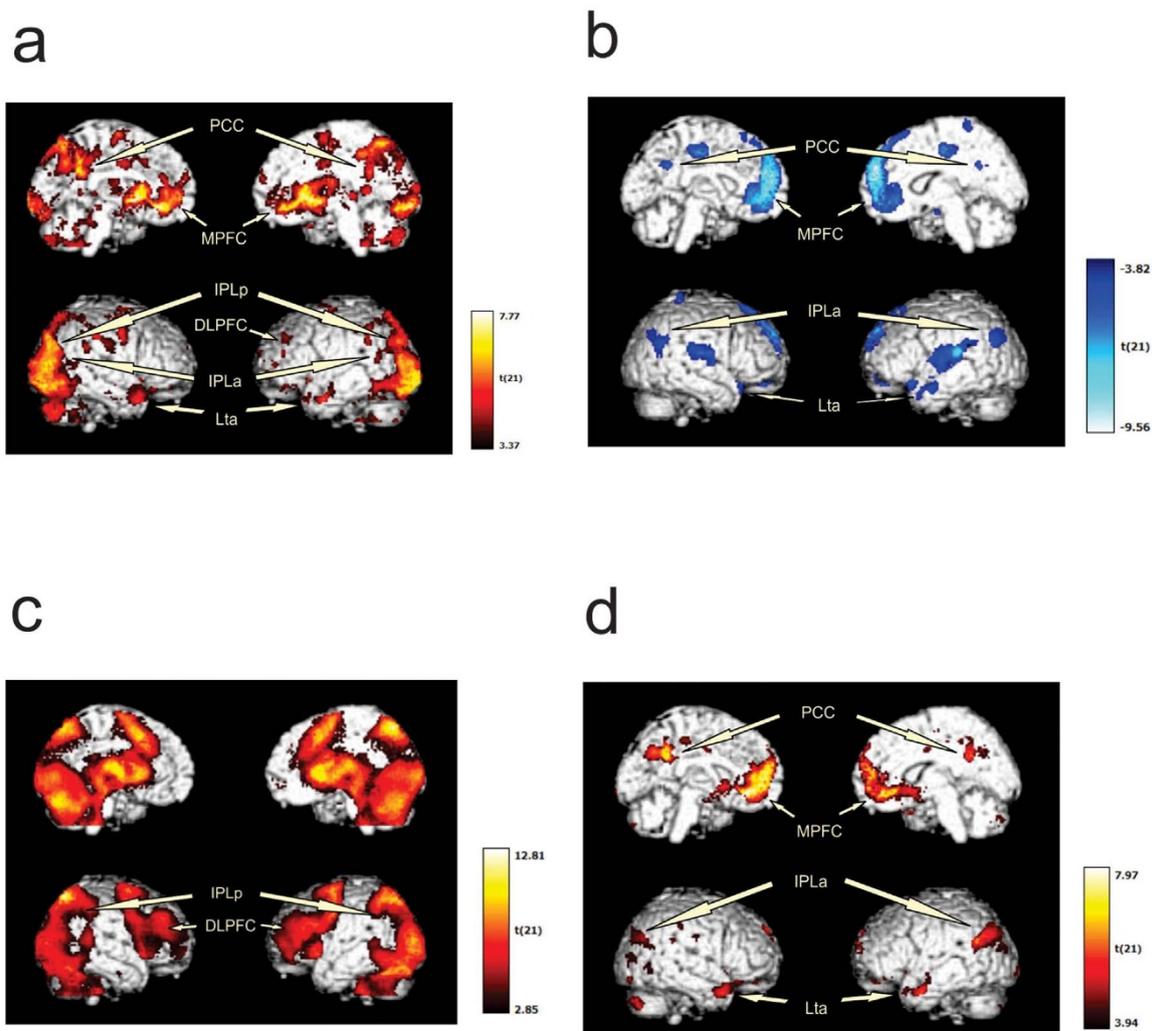


Figure 2 | (a) Regions that showed greater activation during the preparation period for the Dual Task condition than for the Single Task condition (Dual > Single). An FDR ($p = 0.01$) and an extent threshold (10 voxels) were used. (b) Regions that showed lower activation during the execution period for the Dual condition than for the Single condition (Single > Dual). The coordinates are shown in Table 1. (c) Regions that showed greater activation during the execution period for the Dual condition than for the Single condition (Dual > Single). (d) Regions that showed greater activation for the preparation than the execution period for the DUAL than for the Single conditions. [(Dual Preparation – Dual Execution) – (Single Preparation – Single Execution)]. The coordinates are shown in Table 2.

Span Test (RST)⁴⁸ outside the scanner to examine whether or not there is a relationship between individual WM capacity and brain activation. The RST is considered to be one of the standard measures of working memory span⁴⁹, in which participants remember memory items as they read sentences. At various set sizes (2–5), they were asked to recall the memory items. The number of correctly recalled items was recorded as their working memory span score, which could range from 2 to 5.

Results

The mean accuracy and mean response time (RT) data were submitted to one-way Analysis of Variances. There was no difference between the two WM conditions in the accuracy rates for words, $F(1,21) = 2.44$, ns, (96.1% for Category, and 93.8% for Memory). For calculation, there was a significant difference in accuracy rate among conditions, $F(2,42) = 3.40$, $p < .05$, (92.2% for Category, 93.3% for Memory, and 96.4% for Single Task). The calculation accuracy rate was higher for the Single Task condition than for the Category condition, $t(21) = 2.23$, $p < .05$. However, there was no difference between the Category and Memory conditions, $t(21) = 0.92$, ns. RTs were longer for the Category than for the Memory

condition $F(1,42) = 51.74$, $p < 0.01$, (1504 ms for Category, and 1263 ms for Memory). At the post-experimental interview, the participants reported the use of a strategy in which they memorized all the items for both Category and Memory conditions, and tried to find an odd item at the time of response for the Category condition. This strategy seems to cause the pattern of our behavioural results, in which the accuracy rates are the same between the two conditions, but the RTs were slightly longer for the Category condition. There was no difference among the mean RTs for the three conditions for calculation, $F(2,42) = 2.02$, ns.

There was no difference between the Category and Memory conditions in both the preparation and execution periods. Therefore, we compared the mean of the two conditions with the Single condition mean. During the preparation period, the typical DMN regions^{10,12,14,15,33}, including the MPFC, PCC, lateral IPL, lateral temporal, and HF, showed greater activation for the Dual Task than for the Single Task condition as shown in Figure 2-a. No brain region exhibited greater activation for the Single than for the Dual condition. During the task execution period, the same DMN regions, including the MPFC, PCC, lateral IPL, lateral temporal, and HF, showed less activation for the Dual than for the Single condition, as shown in the Table 1 and Figure 2-b.



Table 1 | Regions that showed lower activation for the Dual Task condition than for the Single Task condition (Single > Dual) during the execution period

Cluster	t	Talairach coordinates			BA	Regions
		X	Y	Z		
4957	9.56	10	51	25	9	Superior Frontal Gyrus
1721	7.97	-38	-21	7	13	Insula
1246	7.24	38	-18	19	13	Insula
182	7.12	-53	-69	20	39	Middle Temporal Gyrus
416	7.1	0	-23	44	31	Precuneus
94	6.84	-34	17	-9	47	Inferior Frontal Gyrus
181	6.24	52	-64	24	39	Middle Temporal Gyrus
186	5.08	-2	-53	28	31	Posterior Cingulate Cortex
50	5.07	27	14	-7		Clastrum
122	4.86	-53	-2	-15	21	Middle Temporal Gyrus
30	4.73	25	-10	-12		Parahippocampal gyrus
69	4.63	13	-46	70	7	Postentorial gyrus
23	4.58	-13	15	60	6	Superior Frontal Gyrus
42	4.35	-15	27	55	6	Superior Frontal Gyrus
14	4.2	-47	-5	-4	22	Superior Temporal Gyrus

The brain regions that are typically associated with the WM network, including DLPFC, the anterior cingulate cortex (ACC), and IPL, showed greater activation for the Dual than for the Single condition during the task preparation period as well as the execution period, as shown in Figure 2-a & 2-c.

Results of an interaction analysis are shown in Table 2 and Figure 2-d. These indicate regions where greater activation for the preparation than for the execution period is especially present in the Dual Task condition when compared to the Single Task condition. Thus the value of (Dual Preparation - Dual Execution) - (Single Preparation - Single Execution) is highest in these regions. These DMN regions, including the MPFC, PCC, lateral IPL, LT, and HF, showed greater activation during the preparation period than the execution period because they were activated during the preparation period and deactivated during the execution period.

The percent signal change data for the DMN regions across the time course with the onset of instruction as the reference point are shown in Figure 3. Our goal of this analysis was to obtain converging evidence between the activation data and the percent signal change. We compared the Single and Dual task conditions in the analysis of the activation data; and therefore, we compared each condition with its own baseline for the time course data here. The results were consistent with the fMRI activation data. The hubs of the DMN regions, MPFC and PCC, showed activation during the preparation period; however, during the execution period, all DMN regions except HF showed deactivation. The percent signal change data for the WMN regions are shown in Figure 3. The left DLPFC and left IPL showed activation during the preparation period, and all the WMN regions showed activation during the execution period.

We computed correlation coefficients between individual RST scores (Mean = 3.55, SD = 0.92) and the peaks of the per cent signal change data to see whether or not there is a relationship between individual WM capacity and brain activation. RST scores were marginally correlated with the level of activation in MPFC during the preparation period (left MPFC: $r(20) = 0.376$, $0.05 < p < 0.10$, right MPFC: $r(20) = 0.364$, $0.05 < p < 0.10$). The higher the working memory span, the higher the activation in MPFC during the preparation period. The RST scores were also correlated with activation in the right anterior IPL during the preparation and execution periods (preparation: $r(20) = 0.428$, $p < 0.05$, execution: $r(20) = 0.608$, $p < 0.05$). The higher the RST scores, the higher the activation during the preparation period, and the lower the deactivation during the execution period.

Discussion

The main findings of the present study could be summarized as follows. (1) The core DMN regions (MPFC & PCC) and WMN regions showed activation during task preparation. (2) During execution, the WMN regions stayed activated, but the DMN regions were deactivated.

During task preparation, the hubs of the DMN regions, MPFC and PCC, were activated. However, along with these DMN regions, the WMN was also activated during the preparation period. In the present experiment, the DMN might be involved in the initiation of the task set which also includes the DLPFC and posterior IPL regions of the WMN. Task preparation might consist of several functions. When participants are given a cue to prepare for a task, they might plan strategic actions to engage in successful goal directed behavior²⁰. It is also possible that a part of this preparation is related to prospective memory as well as retrieval of episodic memory of task sets that participants formed in previous trials^{19,20,33}, as reported by some participants in the post-experimental interview. Both aspects of task preparation would seem to implicate the DMN. The WMN regions showed activation during the preparation period because they are the task relevant regions in the execution phase; therefore, these regions are associated with the task set that participants formed. These results seem to similar to the effect of top-down attention which has been shown in previous studies^{25,27,50,51}.

During the execution period, however, activity patterns in the WMN and DMN regions were distinctly opposite. The WMN regions were activated, whereas the DMN regions were deactivated. These results are consistent with previous findings regarding the relationship between the WMN and DMN. In these previous findings, the higher the activation in the WMN, the lower the activation in the DMN^{32,34-39}. In our experiment, the DMN regions showed reduction of activation when attentional resources were allocated to the task relevant working memory regions as the resource demands increased.

In the present study, we also examined whether or not there is a relationship between working memory span and brain activity. We found some indication that higher working memory span is associated with a higher level of activation in the MPFC during task preparation. This might be related to previous findings such as the one by Sternberg⁵², who showed that people with higher intelligence tend to spend more time in preparing for tasks than people with lower intelligence. However, this point needs further investigation because the correlations were only marginally significant. During the



Table 2 | Regions that showed greater activation for the preparation than the execution period for the Dual Task than for the Single Task conditions. [(Dual Preparation – Dual Execution) – (Single Preparation – Single Execution)]

Cluster	t	Talairach coordinates			BA	Regions
		X	Y	Z		
3800	7.97	-6	34	4	24	Anterior Cingulate
202	6.65	46	15	-15	38	Superior Temporal Gyrus
998	6.59	-7	-65	30	7	Occipital Gyrus/Cuneus
642	6.03	-50	-73	22	39	Middle Temporal Gyrus
336	5.94	-21	9	-4	SC	Lentiform, Putamen
218	5.9	-51	-3	-19	21	Middle Temporal Gyrus
154	5.69	43	-74	27	39	Middle Temporal Gyrus
16	5.27	-40	-29	-3	22	Insula
23	5.01	41	-42	24	13	Insula
153	4.97	27	-70	-34		Cerebellum
29	4.74	41	-79	6	19	Middle Occipital Gyrus
37	4.6	2	-11	36	24	Posterior Cingulate Cortex
23	4.59	32	-81	-17		Cerebellum
17	4.59	-14	-98	-9	17	Occipital, Lingual Gyrus
21	4.53	52	-64	3	37	Middle Temporal Gyrus
11	4.43	-14	-76	-41		Cerebellum
25	4.41	38	-19	25	13	Insula
18	4.38	20	-24	53	4	Precentral
14	4.38	9	-43	40	31	Posterior Cingulate Cortex
17	4.31	58	-38	43	40	Inferior Parietal Lobe
13	4.3	-27	-94	-12	18	Fusiform gyrus
51	4.29	-7	-34	42	7	Precuneus
12	4.27	60	-20	32	2	Postcentral Gyrus

execution period of the present study, significant correlations were also found between working memory span and the right anterior IPL, which is a part of the DMN. The higher the RST scores, the higher the activation during the preparation period, and the lower the deactivation during the execution period. The lower level of deactivation during execution in the anterior IPL might be related to the capacity of the processing resources. People with high working memory span might have more processing capacity; and therefore, such individuals may show less reduction of activation during task execution. This pattern is consistent with the results of Lipp et al.⁵³, in which they found that more intelligent individuals show less deactivation of the posterior cingulate/precuneus as compared to less intelligent people.

In the present study, the HF showed a slightly different pattern of activation and deactivation than the other DMN regions. HF showed activation during the preparation period, along with the other DMN regions. However, the HF continued its activation into the execution period, as shown in the percent signal change data. This was the case even though one part of HF (parahippocampal gyrus) showed deactivation during the execution period (see Table 1). Interestingly, this pattern is consistent with findings of previous studies that found HF activation associated with WM maintenance^{54,55}. Therefore, in our data, the HF seems to have worked with the other DMN regions during the preparation period, but not during the execution period, probably because of the roles it has in working memory. In this respect, our results are consistent with previous findings suggesting that the DMN regions do not always work together, and their activity depends on task requirements¹⁹. Another possible explanation for this pattern is that there might be functional subdivisions in brain regions. Functional subdivisions have been suggested especially in large areas such as the anterior PFC (BA10)^{56,57}, and ACC⁵⁸. In the present study, we observed another functional subdivision in the IPL (BA 40). The anterior region (IPLa) worked together with the other regions of the DMN whereas the posterior region (IPLp) functioned as a part of the WMN.

In conclusion, we replicated and extended our previous findings in the present study. We found that the MPFC and PCC, which are the hubs of the DMN regions were activated during task preparation.

However, given the small difference between the conditions in the percent signal change data, our conclusions should be considered tentative. WMN regions were also activated during task preparation. These results show that activity in the DMN and WMN regions are not necessarily negatively correlated, but could be coactive depending on task requirements and available attentional resources. In the present study, it is possible that the DMN was involved in the initiation of episodic memory retrieval of the task set and that this retrieval process also involved the WMN. However, the WMN stayed activated while the DMN was deactivated during task execution. The results suggest that the DMN regions are deactivated due to reallocation of attentional resources to the task relevant regions as task demands increase.

Methods

Participants. Twenty four students from the Kyoto area, (age ranges from 19 to 33 years; 6 females, 3 left-handers) participated as paid volunteers. Two participants were excluded from data analysis because of excessive head motion. All had normal or corrected-to-normal vision. The participants gave the written informed consent that was approved by the institutional review board of the Advanced Telecommunications Research Institute International (ATR). The experiment was conducted in accordance with the guidelines and regulations approved by the ATR Brain Imaging Centre Review Board.

Stimuli and design. We used a dual task procedure, in which a primary task was a verbal WM task, and a secondary task was addition of digits. In the WM task, participants were presented with four words. We set up two conditions for the WM task: Category and Memory. In the Category condition, there is always one odd item, that is an item that does not form a group with the other three words (e.g., Congress, Minister, Politics, Company), and the participants were asked to find the odd item. In the Memory condition, they were required to remember the four words. The words were taken from the subtest of the Kyoto-University NX Intelligence Scale⁵⁹. The Category and Memory conditions were dual tasks, in which the participants also performed addition. A background task was simple addition of four single-digits presented successively one at a time at the centre of the screen, and participants always performed addition. There was also a Single Task condition, in which the participants performed only addition and ignored the words.

Procedure. An experimental procedure was basically the same as our previous study¹⁷. At the beginning of each trial, a visual instruction was given regarding the conditions (Category, Memory, or Single Task), followed by a six-second delay (Preparation period). The participants were told to prepare for the task by forming a

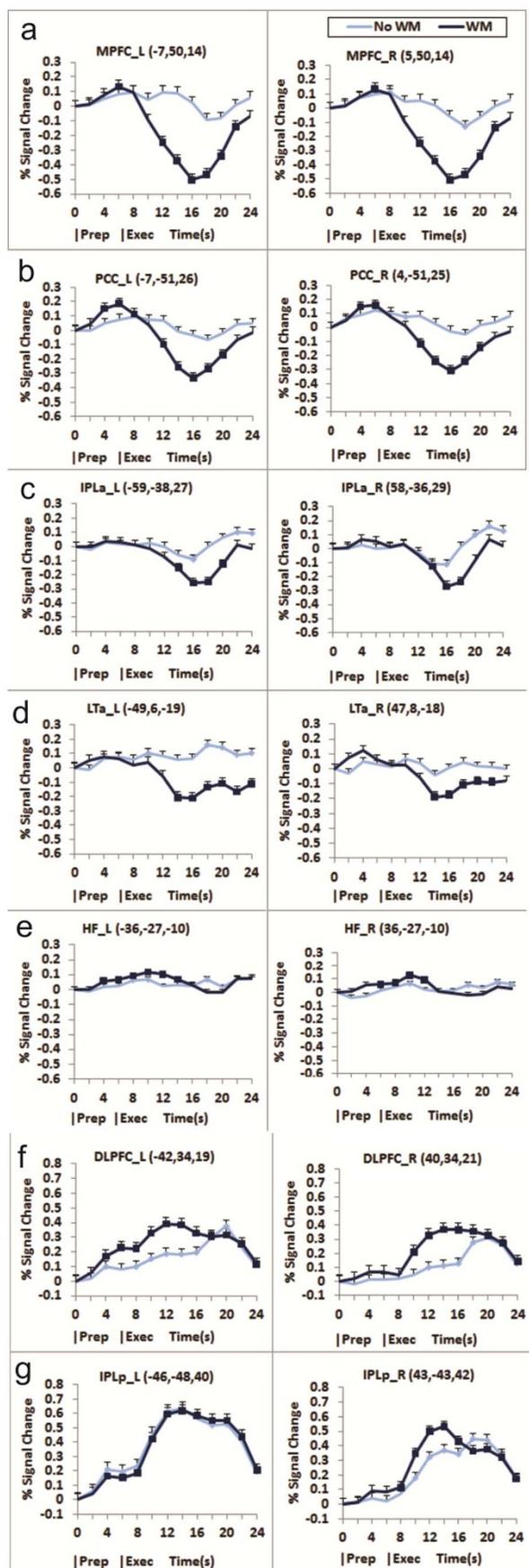


Figure 3 | Signal change (%) of the DMN and WMN regions across the time course with the stimulus onset as a baseline. (a) anterior medial prefrontal cortex (MPFC), (b) posterior cingulate (PCC), (c) anterior IPL (IPLa), (d) lateral temporal (LT), and (e) hippocampal formation (HF).

All WMN regions showed activation for the DUAL condition during the execution period. (f) dorsolateral prefrontal cortex (DLPPFC), and (g) posterior IPL (IPLp). The central coordinates for each ROI is shown inside the parentheses. Error bars denote the standard error of the mean. The 99% confidence interval was computed with the following formula. $.99CI = \text{Mean psc} + \text{critical } t \text{ value} \times \text{standard error}$, in which the standard error was computed by the square root of the Mean Square Error/N. The mean square error was taken from the ANOVA. The large data points indicate the points that the 99% confidence interval did not include zero. The small data points indicate those points that the 99% confidence interval included zero.

task set for the Category and Memory conditions, whereas, they were told that they don't need to form a set and ignore the words for the Single Task condition. Then an execution period began, in which the stimulus words were presented for six seconds and four single-digits also appeared one at a time at the centre of the display. Participants had to add the digits and remember the final answer. After a two second delay period, a probe word appeared. For the Category condition, the participants had to judge whether or not the probe word was an odd item. For the Memory condition, they had to judge whether or not the probe word was among the four words previously presented. For the Single Task condition, the participants were told to ignore the stimulus words while performing the addition, and to determine the number of letters in the probe word when it was introduced. In the final step of the trial for all three conditions, a two-digit number appeared and participants judged whether or not the number was the answer to the addition problem. At the end of each trial, an inter trial interval of 6, 8, or 10 seconds was randomly inserted. An example of a trial sequence is shown in Figure 1. Stimuli were projected onto a viewing screen attached within the bore of the scanner. Stimulus presentation and behavioural data collection were controlled with the Presentation software (Neurobehavioral Systems Inc., Albany, CA, USA). Each participant received a separate practice session before the MRI session. There were 16 trials for each condition, presented in a random order.

fMRI data acquisition and analysis. Whole brain imaging data were acquired on a 3-T whole-body magnetic resonance imaging scanner (MAGNETOM Trio, A Tim System (3T), Siemens) at ATR. For functional imaging, we used a gradient-echo echo-planar imaging sequence with the following parameters: TR = 2000 ms, TE = 30 ms, flip angle = 80°, FOV = 192 mm × 192 mm, and pixel matrix = 64 × 64, with 3 × 3 × 5 mm voxels. Thirty slice images were taken with 5 mm slice thickness in an oblique-axial plane.

After collection of functional images, T1-weighted images (191 slices with no gap), using a conventional spin-echo pulse sequence (TR = 2250 ms, TE = 3.06 ms, flip angle = 9°, FOV = 256 mm × 256 mm, and pixel matrix = 256 × 256, with voxel size 1 × 1 × 1 mm), were collected for anatomical co-registration. After image construction, functional images were analysed using SPM5 (Wellcome Department of Cognitive Neurology, University College London, UK). Preprocessing contained slice timing correction, motion correction, normalization to EPI and spatial smoothing with an 8-mm Gaussian kernel. In a statistical model, we included separate covariates for the instruction of each condition (Category, Memory, and Addition), and one covariate for the presentation of word stimuli. We convolved those covariates with a hemodynamic response function (HRF).

Event duration for the preparation period was 0, whereas that for the execution period was 6. The selection of event duration was based on expected length of cognitive processes. According to results of interviews after the scan, most participants reported that they selected their preferred strategies in response to instruction cues. Therefore, preparation seems to be implemented at the beginning of the preparation phase. On the other hand, experimental stimuli were presented through the execution phase and participants needed to focus on them; therefore, working memory should be active throughout the execution phase. There were three regressors for the execution period, corresponding to the experimental conditions. No significant correlation was observed among regressors between the preparation period and execution period in each condition, indicating no collinearity among regressors. An FDR ($p = 0.01$) and an extent threshold (10 voxels) were used. There was no difference between the Memory and Category conditions in terms of fMRI activation as well as the accuracy of performance. During the post-experimental interviews, the participants reported that they used a strategy in which they memorized all stimulus items for both the Category and Memory conditions, and tried to find an odd item at the time of response for the Category condition. This strategy seemed to cause the same pattern of performance between the Category and Memory conditions during the preparation and execution periods. Therefore, we combined the Category and Memory conditions, and named it a Dual Task condition. We then compared the Dual Task condition with the Single Task (addition only) condition in the analyses.

Regions of interests (ROI) and percent signal change. Our main purpose of the ROI analysis and percent signal change was to obtain converging evidence between the activation data and the percent signal change. The activation data were based on differences of the fit in the general linear model between the dual and single task conditions. Here, we examined patterns of activation and deactivation for the major DMN and WMN regions compared to their own baseline (the onset of the



- instruction). Fourteen functional ROIs (ten ROIs for the DMN and four ROIs for the WMN) were defined based on the fMRI activation data in the same way as our previous study⁴⁷. Ten ROIs for the DMN were defined based on activation during the preparation period and deactivation during the execution periods, also with reference to the coordinates of the DMN regions in the preceding studies^{10,14,37}. Four ROIs for the WMN were based on the activation during the preparation and execution periods. A sphere was created for each cluster with the radius of 3–4 mm to maximize the coverage of the region. The functional ROIs were all bilateral, including the medial prefrontal cortex (MPFC, BA10), posterior cingulate cortex (PCC, BA31), anterior inferior parietal lobe (IPLa, BA40), posterior lateral temporal lobe (LTp, BA39), and hippocampal formation (HF) for the DMN. For the WMN, the dorsolateral prefrontal cortex (DLPFC, BA46) and a posterior inferior region of the parietal lobe (IPLp, BA40) were selected. The latter region is more posterior than the location of the IPLa that was included in the DMN. The coordinates of the centre of ROIs are shown in Figure 3. The activation time course for each ROI was then extracted separately for each participant for each condition using the MarsBar⁶⁰. A percent signal change (psc) was computed for each ROI relative to the onset of the instruction (0 sec) to examine activation and deactivation compared to its own baseline. A 99% confidence interval was computed for each data point to examine whether or not each data point is different from the baseline (psc = 0).
- Bressler, S. L. & Menon, V. Large-scale brain networks in cognition: emerging methods and principles. *Trends Cogn. Sci.* **14**, 277–90 (2010).
 - Damoiseaux, J. S. *et al.* Consistent resting-state networks across healthy subjects. *Proc. Natl. Acad. Sci. USA* **103**, 13848–13853 (2006).
 - Deco, G. & Corbetta, M. The Dynamical Balance of the Brain at Rest. *Neurosci.* **17**, 107–123 (2011).
 - Niendam, T. A., Laird, A. R., Ray, K. L., Dean, Y. M. & Carter, C. S. Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. *Cogn. Affect. Behav. Neurosci.* **12**, 241–268 (2012).
 - Seeley, W. W. *et al.* Dissociable intrinsic connectivity networks for salience processing and executive control. *J. Neurosci.* **27**, 2349–56 (2007).
 - Toro, R., Fox, P. T. & Paus, T. Functional coactivation map of the human brain. *Cereb. Cortex* **18**, 2553–9 (2008).
 - Van den Heuvel, M. P., Stam, C. J., Kahn, R. S. & Hulshoff Pol, H. E. Efficiency of functional brain networks and intellectual performance. *J. Neurosci.* **29**, 7619–24 (2009).
 - Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E. & Buckner, R. L. Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *J. Neurophysiol.* **100**, 3328–42 (2008).
 - Spreng, R. N., Stevens, W. D., Chamberlain, J. P., Gilmore, A. W. & Schacter, D. L. Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. *Neuroimage* **53**, 303–17 (2010).
 - Binder, J. R. *et al.* Conceptual processing during the conscious resting state. A functional MRI study. *J. Cogn. Neurosci.* **11**, 80–95 (1999).
 - Gusnard, D. A. & Raichle, M. E. Searching for a baseline: Functional imaging and the resting human brain. *Nat. Rev. Neurosci.* **2**, 685–694 (2001).
 - Mazoyer, B. *et al.* Cortical networks for working memory and executive functions sustain the conscious resting state in man. *Brain Res. Bull.* **54**, 287–98 (2001).
 - McKiernan, K. A., Kaufman, J. N., Kucera-Thompson, J. & Binder, J. R. A parametric manipulation of factors affecting task-induced deactivation in functional neuroimaging. *J. Cogn. Neurosci.* **15**, 394–408 (2003).
 - Raichle, M. E. *et al.* A default mode of brain function. *Proc. Natl. Acad. Sci. U. S. A.* **98**, 676–82 (2001).
 - Shulman, G. L. *et al.* Common Blood Flow Changes across Visual Tasks: II. Decreases in Cerebral Cortex. *J. Cogn. Neurosci.* **9**, 648–63 (1997).
 - Sridharan, D., Levitin, D. J. & Menon, V. A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 12569–74 (2008).
 - Christoff, K., Ream, J. M., Geddes, L. P. T. & Gabrieli, J. D. E. Evaluating self-generated information: anterior prefrontal contributions to human cognition. *Behav. Neurosci.* **117**, 1161–8 (2003).
 - Mason, M. F. *et al.* Comment on “Wandering minds: the default network and stimulus-independent thought” *Science* (80-.). **317**, 43; author reply 43 (2007).
 - Sestieri, C., Corbetta, M., Romani, G. L. & Shulman, G. L. Episodic memory retrieval, parietal cortex, and the default mode network: functional and topographic analyses. *J. Neurosci.* **31**, 4407–20 (2011).
 - Spreng, R. N., Mar, R. A. & Kim, A. S. N. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J. Cogn. Neurosci.* **21**, 489–510 (2008).
 - Andrews-Hanna, J. R. The brain’s default network and its adaptive role in internal mentation. *Neuroscientist* **18**, 251–70 (2012).
 - Spreng, R. N. & Grady, C. L. Patterns of brain activity supporting autobiographical memory, prospection, and theory of mind, and their relationship to the default mode network. *J. Cogn. Neurosci.* **22**, 1112–23 (2010).
 - Corbetta, M. & Shulman, G. L. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* **3**, 201–15 (2002).
 - Corbetta, M., Patel, G. & Shulman, G. L. The reorienting system of the human brain: From environment to theory of mind. *Neuron* **58**, 306–324 (2008).
 - Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T. & D’Esposito, M. Top-down enhancement and suppression of the magnitude and speed of neural activity. *J. Cogn. Neurosci.* **17**, 507–17 (2005).
 - Kastner, S. & Ungerleider, L. G. Mechanisms of visual attention in the human cortex. *Annu. Rev. Neurosci.* **23**, 315–341 (2000).
 - Pessoa, L., Kastner, S. & Ungerleider, L. G. Neuroimaging studies of attention: from modulation of sensory processing to top-down control. *J. Neurosci.* **23**, 3990–8 (2003).
 - Shmuel, A., Augath, M., Oeltermann, A. & Logothetis, N. K. Negative functional MRI response correlates with decreases in neuronal activity in monkey visual area V1. *Nat. Neurosci.* **9**, 569–77 (2006).
 - Persson, J., Lustig, C., Nelson, J. K. & Reuter-Lorenz, P. A. Age differences in deactivation: a link to cognitive control? *J. Cogn. Neurosci.* **19**, 1021–32 (2007).
 - Daselaar, S. M., Prince, S. E. & Cabeza, R. When less means more: deactivations during encoding that predict subsequent memory. *Neuroimage* **23**, 921–7 (2004).
 - Kelly, A. M. C., Uddin, L. Q., Biswal, B. B., Castellanos, F. X. & Milham, M. P. Competition between functional brain networks mediates behavioral variability. *Neuroimage* **39**, 527–37 (2008).
 - Weissman, D. H., Roberts, K. C., Visscher, K. M. & Woldorff, M. G. The neural bases of momentary lapses in attention. *Nat. Neurosci.* **9**, 971–8 (2006).
 - Buckner, R. L., Andrews-Hanna, J. R. & Schacter, D. L. The brain’s default network: anatomy, function, and relevance to disease. *Ann. N. Y. Acad. Sci.* **1124**, 1–38 (2008).
 - Christoff, K., Gordon, A. M., Smallwood, J., Smith, R. & Schooler, J. W. Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 8719–24 (2009).
 - Fox, M. D. *et al.* The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 9673–8 (2005).
 - Fransson, P. Spontaneous low-frequency BOLD signal fluctuations: an fMRI investigation of the resting-state default mode of brain function hypothesis. *Hum. Brain Mapp.* **26**, 15–29 (2005).
 - Greicius, M. D., Krasnow, B., Reiss, A. L. & Menon, V. Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* **100**, 253–8 (2003).
 - Pyka, M. *et al.* Impact of working memory load on fMRI resting state pattern in subsequent resting phases. *PLoS One* **4**, e7198 (2009).
 - Tomasi, D., Ernst, T., Caparelli, E. C. & Chang, L. Common deactivation patterns during working memory and visual attention tasks: an intra-subject fMRI study at 4 Tesla. *Hum. Brain Mapp.* **27**, 694–705 (2006).
 - Mayer, J. S., Roebroeck, A., Maurer, K. & Linden, D. E. J. Specialization in the default mode: Task-induced brain deactivations dissociate between visual working memory and attention. *Hum. Brain Mapp.* **31**, 126–39 (2010).
 - Chadick, J. Z. & Gazzaley, A. Differential coupling of visual cortex with default or frontal-parietal network based on goals. *Nat. Neurosci.* **14**, 830–2 (2011).
 - Gerlach, K. D., Spreng, R. N., Gilmore, A. W. & Schacter, D. L. Solving future problems: default network and executive activity associated with goal-directed mental simulations. *Neuroimage* **55**, 1816–24 (2011).
 - Ellamil, M., Dobson, C., Beeman, M. & Christoff, K. Evaluative and generative modes of thought during the creative process. *Neuroimage* **59**, 1783–94 (2012).
 - Meyer, M. L., Spunt, R. P., Berkman, E. T., Taylor, S. E. & Lieberman, M. D. Evidence for social working memory from a parametric functional MRI study. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 1883–8 (2012).
 - Summerfield, C. & Egner, T. Expectation (and attention) in visual cognition. *Trends Cogn. Sci.* **13**, 403–9 (2009).
 - Anticevic, A., Repovs, G., Shulman, G. L. & Barch, D. M. When less is more: TPJ and default network deactivation during encoding predicts working memory performance. *Neuroimage* **49**, 2638–48 (2010).
 - Koshino, H. *et al.* Anterior Medial Prefrontal Cortex Exhibits Activation during Task Preparation but Deactivation during Task Execution. *PLoS One* **6**, 11 (2011).
 - Osaka, M. & Osaka, N. Working memory capacity related to reading: a measurement with the Japanese version of reading span test. *Japanese J. Psychol.* **65**, 339–345 (1994).
 - Daneman, M. & Carpenter, P. A. Individual Differences in Working Memory and Reading. *J. Verbal Learning Verbal Behav.* **19**, 450–466 (1980).
 - Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R. & Ungerleider, L. G. Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* **22**, 751–61 (1999).
 - Miller, B. T. & D’Esposito, M. Searching for “the top” in top-down control. *Neuron* **48**, 535–8 (2005).
 - Sternberg, R. J. Intelligence and Nonentrenchment. *J. Educ. Psychol.* **73**, 1–16 (1981).
 - Lipp, I. *et al.* Investigating Neural Efficiency in the Visuo-Spatial Domain: An fmri Study. *PLoS One* **7**, e51316 (2012).
 - Axmacher, N. *et al.* Sustained neural activity patterns during working memory in the human medial temporal lobe. *J. Neurosci.* **27**, 7807–16 (2007).
 - Ranganath, C. & Esposito, M. D. Medial temporal lobe activity associated with active maintenance of novel information. *Neuron* **31**, 865–873 (2001).
 - Burgess, P. W., Gilbert, S. J. & Dumontheil, I. The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends Cogn. Sci.* **11**, 290–298 (2007).
 - Gilbert, S. J. *et al.* Functional specialization within rostral prefrontal cortex (area 10): a meta-analysis. *J. Cogn. Neurosci.* **18**, 932–48 (2006).



58. Bush, G., Luu, P. & Posner, M. I. Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn. Sci.* **4**, 215–222 (2000).
59. Kuraishi, S., Osaka, R., Utsugi, S. & Umemoto, T. *Kyoto-University NX Intelligence Scale*. (Success Bell Co.,Ltd. Edajima, Hiroshima, Japan, 1955).
60. Brett, M., Anton, J.-L., Valabregue, R. & Poline, J.-B. Region of interest analysis using an SPM toolbox. *Neuroimage* **16** (2002).

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Author contributions

H.K., T.M., K.Y., M.O. and N.O. conceived the study and participated in the design. T.M. and K.Y. performed data collection and data analysis. H.K., T.M., K.Y., M.O. and N.O.

participated in the data interpretation. H.K. wrote the first draft. H.K., T.M., K.Y., M.O. and N.O. read and approved the final manuscript.

Additional information

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