Differences in Regional Brain Activities during Memory Acquisition Depending on Individual Working Memory Capacity

Hong-Seng GAN,*, ** Tatsuya SUZUKI,*** Koichi YOKOSAWA,† Yumie ONO*, #

Abstract  Individual capacity of recall memory varies greatly even among healthy young adults. Nevertheless, the difference in brain circuitry underlying varied memory capacity has yet to be fully investigated. We acquired electroencephalographic measurements from 43 healthy young adults while performing a demanding working memory task and studied the changes in regional cortical activity in relation to different levels of memory performance. The memory task involved sequentially presenting seven arrow pictures to a participant during the encoding period, who was then asked to recall the direction of one of the arrows in the sequence within the retrieval period. We divided the participants into three groups of high, intermediate, and low performance based on the weighted hierarchical grouping method. Regional brain activities were source-localized using multiple sparse priors method in the high- and low-performance groups, and group differences were determined by non-parametric permutation tests. Our findings showed that participants with higher memory performance exhibited wider distribution of cortical activity including the prefrontal and parieto-posterior cortices, whereas lower performance participants only exhibited stable activations across occipital regions. The results implied the importance of selective attention in order to attain optimal individual working memory performance. Furthermore, we suggest the potential role of the angular gyrus as an interplay between the prefrontal and posterior regions for the management of stimulus flow and signal control. Future works should focus on conducting more thorough connectivity analysis to investigate the relationship of cortical activations with individual working memory performance.

Keywords: electroencephalography, working memory, source localization, top-down modulation, individual differences.


1. Introduction

Individual working memory (WM) capacity is limited but not fixed. Understanding the cortical changes across varied WM capacities of healthy individuals may reveal potential biomarkers for various high-level cognitive functions [1]. WM is broadly perceived to be regulated by a central executive component located in the prefrontal cortex (PFC), which is identified as the decision-making unit of WM modulation [2]. Executive circuitry within the PFC is responsible for maintaining behavioral goals such as task rules and adaptively encoding task-relevant information held in WM [3]. Then, different sensory information is assigned to various content-specific buffers across parieto-posterior regions. This memory-related brain circuitry is supported by several studies [4, 5], which indicate that the lateral PFC (lPFC) has a role in guiding the extrastriate cortex to accomplish goal-relevant representation by passing down sensorimotor signals to different sensory buffers for storage or temporary retention.

However, the extensive connections between the PFC and parieto-posterior regions during the memory process remain to be explored. Results from substantial electrophysiological and imaging studies [6, 7] have shown that successful encoding of low-level visual stimulus features such as image orientation and object identi-
ty occur in the early visual cortex but not the PFC, suggesting that the subregions of the posterior cortices are highly specialized to mediate low-level visual features or identify task stimuli. Intriguingly, it is widely anticipated that close interconnection exists between the neural populations of these two regions. In particular, control and attentional information may flow from the frontoparietal to the visual cortex, concurrent with another reverse mechanism that transmits sensory information from the visual cortex to the parietal and PFC, forming a bidirectional sensorimotor processing model driven by goal-oriented attention [8] to attain successful memory encoding.

Despite numerous studies showing interactions among various cortical regions, there is hardly any consensus on the precise brain machinery under the influence of varied WM capacity [9]. In this paper, we calculated the accuracy for every recall item in a memory task and conducted a localized brain activity analysis in participants with higher and lower performance to reveal the cortical machinery involved in these groups.

2. Methods

2.1 Participants

Forty-three healthy adults (21 men, 22 women, 21.6 ± 0.2 years of age, all right-handed) with normal or corrected-to-normal vision were recruited from Meiji University to participate in the experiment. The study was approved by the Institutional Review Board and all participants provided written informed consent for participation.

2.2 Behavioral Task

Electroencephalograms (EEG) of the participants were acquired using a bioamplifier (g.USBamp, g.tec Medical Engineering GmbH, Schiedlberg, Austria) with a 256 Hz sampling rate and 0.5–100 Hz bandpass filter. Thirty-two active electrodes were attached to the head of the participant at Fp1, Fp2, AF3, AF4, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO7, POz, P08, O1, and O2 of the standard 10% EEG layout using an electrode cap. Additional ground and reference electrodes were attached to AFz and the right earlobe, respectively.

Participants sat on a chair 60 cm away from the fixation point. Their right hands were positioned on a response keypad to perform the sequential visual WM task (Fig. 1) [10, 11]. Each trial consisted of an encoding and a retrieval period. During the encoding period, participants were presented a series of seven arrows (with arrowhead pointing up, down, right, or left) for a duration of 100 ms each with 500-ms intervals. Each arrow was presented on central visual field and was 2 cm away from the fixation point (visual angle equaled to 1°). They were instructed to remember the sequence of the arrow directions. Every encoding period was followed by a retrieval period, in which the participants were randomly assigned a numerical cue, n, and were required to report the direction of the n-th arrow presented in the preceding encoding period by pressing one of the four arrow keys on the keypad. A single session consisted of 70 of these WM trials. The session was repeated twice continuously with a short break in between. Consequently, a total of 140 WM trials were acquired from each participant.

The advantage of our WM task is the minimization of false positive responses. The chance ratio of the correct responses is lower (25%) compared to the yes/no-type response (50%). The different nature of the encoding items (arrow direction) and the retrieval cue (numerical figure) requires higher cognitive processes of simultaneously transferring the visual cue into the information of direction and updating the encoded sequence, which is beneficial to investigate the regional cortical activity during the active state of WM function. In addition, the difficulty of the task can be adjusted by changing the number of arrows in a single sequence. We adopted a seven-arrow sequence from our preliminary experiment, so that the mean accuracy rate would be approximately 70%.

2.3 EEG preprocessing and source localization

EEG data were first converted and divided into trials us-
ing EEGLAB [12] for source-localization analysis using the Statistical Parametric Mapping (SPM) 8 software (Wellcome Trust, London, UK). Trials contaminated with eye/movement artifacts and exceeding $\pm 100\, \mu V$ were excluded from further analyses. The regional brain activity corresponding to the oscillatory EEG activity in the alpha band (8–13 Hz) during the encoding period was investigated using multiple sparse priors (MSP) [13], which was implemented on SPM 8. Alpha-band activity was selected because it is one of the signature oscillatory activities that are modulated during memory storage [10]. MSP is an EEG source-localization technique that utilizes hierarchical and empirical Bayes models to reconstruct distributed electrical neural activity. The 3D source reconstruction was performed with a ‘normal’ mesh model, in which 8196 current dipoles were assumed in the gray matter. EEG data were co-registered to the template brain based on the default MNI coordinates of the 32-channel EEG electrode layout. The boundary element method (EEG BEM) was used for forward model generation. MSP was applied to the band-pass filtered EEG data (8–13 Hz) for the whole encoding period of each epoch without any prior information or restriction of source locations. The distribution of current amplitudes in the normalized brain coordinates (voxel size: $2 \times 2 \times 2\, \text{mm}^3$) was estimated for all trials of all participants. One-sample $t$-test was applied to 140 source-localized images of each individual [one tailed; $p < 0.05$, family-wise error (FWE) corrected, cluster threshold $k > 8$] to determine common regional activities. The resultant current distribution images were subjected to the second-level group analysis described below.

### 2.4 Group Analysis
Participants were divided into high-, intermediate-, and low-performance groups depending on their mean accuracy rates in the WM trials for recall numbers 3–5, which showed the lowest overall memory accuracy of $61.1 \pm 17.5\%$, compared to recall numbers 1–2 (69.8 $\pm$ 17.0%) and 6–7 (83.8 $\pm$ 14.8%). We expected more prominent accuracy differences among the performance groups. A hierarchical grouping method (weighted pair-group method using arithmetic averages) [14] was adopted for the cluster analysis. For group analysis, we used the regional brain-activity data of the high- and low-performance groups to highlight clear contrast of cortical activation between two sets of distinctly different memory capacities, with the intermediate-performance group acting as a buffer. The common cortical activity patterns within each group and differences in cortical activity patterns between groups were computed using one-sample and two-sample non-parametric permutation tests, respectively (SnPM toolbox; University of Warwick, Coventry, UK) [15]. Permutation tests were employed to confirm the robustness of the detected cortical changes. We adopted 5,000 permutations per trial with a default cluster-forming threshold ($p = 0.01$; uncorrected). A cluster-based FWE correction ($p < 0.05; k > 8$) was further applied to extract statistically significant regional activity. Besides the voxel-based analysis, we also performed region-of-interest (ROI) analysis focusing on the PFC region (bilateral BA 9, 10, and 46) to compare total electrical activities between high- and low-performance groups by two-sample $t$-test, to further investigate the reason for the lack of statistically significant group differences in the PFC regions from voxel-based statistics as shown below.

### 3. Results

#### 3.1 Behavioral Analysis
Figure 2 shows the averaged accuracy rates of memory recall of sequential directional arrows in our WM task. Hierarchical grouping divided 43 participants into three groups: eight high- ($87.9 \pm 4.7\%$), 20 intermediate-
(64.7 ± 7.6%), and 15 low- (43.3 ± 6.3%) performance. Overall performance showed that the beginning (74.5 ± 18.8%) and ending (91.3 ± 14.2%) sections of the memory task were well memorized by the participants. Meanwhile, the accuracy of memory recall was lowest for the middle items of the memory task (Recall number 3: 62.7 ± 19.4%; Recall number 4: 57.6 ± 19.2%; Recall number 5: 60.1 ± 21.3%).

Likewise, a U-pattern was observed in the high-performance group with the lowest accuracy for Recall number 3 (78.8 ± 9.9%). Results from the low-performance group, on the other hand, showed that participants with low recall accuracy tended to remember directional arrows at the end of the sequence (Recall number 6: 48.9 ± 8.9%; Recall number 7: 55.8 ± 8.0%).

### 3.2 EEG Analyses

Figures 3 and 4 illustrate the cortical activations across the brains of participants with higher and lower memory performance, respectively. The activated regions are summarized in Tables 1 and 2. Increased brain activities were selectively observed at the dorsolateral PFC (dLPFC) [Brodmann area (BA) 46], bilateral premotor cortices (BA 6), bilateral frontal poles (BA 10), associative visual cortices (BA 19) and angular gyrus (BA 39) in participants with higher recall accuracy. Meanwhile, similar enhanced brain activities at several brain regions were observed in both the high- and low-performance groups, which included the secondary visual cortex (BA 18) and bilateral temporal cortices (BAs 21 and 22).

The enhanced cortical activations in participants with higher memory performance relative to those with lower memory performance are shown in Fig. 5. The activated regions are summarized in Table 1.

#### Table 1: Summary of significantly activated foci and voxel size in the high-performance group (one-sample t-test).

<table>
<thead>
<tr>
<th>MNI coordinates (mm)</th>
<th>Voxel size</th>
<th>Cortical regions</th>
<th>Brodmann areas</th>
</tr>
</thead>
<tbody>
<tr>
<td>−6</td>
<td>8</td>
<td>68</td>
<td>Premotor cortex</td>
</tr>
<tr>
<td>50</td>
<td>36</td>
<td>4</td>
<td>Dorsolateral prefrontal cortex</td>
</tr>
<tr>
<td>−46</td>
<td>40</td>
<td>2</td>
<td>Frontal pole</td>
</tr>
<tr>
<td>−26</td>
<td>58</td>
<td>−4</td>
<td>Frontal pole</td>
</tr>
<tr>
<td>22</td>
<td>62</td>
<td>12</td>
<td>Frontal pole</td>
</tr>
<tr>
<td>−44</td>
<td>−72</td>
<td>10</td>
<td>Associative visual cortex</td>
</tr>
<tr>
<td>−4</td>
<td>−78</td>
<td>20</td>
<td>Secondary visual cortex</td>
</tr>
<tr>
<td>12</td>
<td>−92</td>
<td>−8</td>
<td>Angular gyrus</td>
</tr>
<tr>
<td>28</td>
<td>−62</td>
<td>44</td>
<td>Angular gyrus</td>
</tr>
<tr>
<td>56</td>
<td>−40</td>
<td>−26</td>
<td>Inferior temporal gyrus</td>
</tr>
<tr>
<td>−58</td>
<td>−10</td>
<td>0</td>
<td>Superior temporal gyrus</td>
</tr>
<tr>
<td>52</td>
<td>−12</td>
<td>−10</td>
<td>Superior temporal gyrus</td>
</tr>
<tr>
<td>46</td>
<td>−30</td>
<td>−4</td>
<td>Middle temporal gyrus</td>
</tr>
</tbody>
</table>
atomical information of the detected cortical areas is summarized in Table 3. In the high-performance group, enhanced brain activities were found in the visual cortices (BA 19) and fusiform gyrus (BA 37) when compared with the low-performance group. No cortical regions showed significantly enhanced activity in participants with lower memory performance relative to those with higher memory performance. The ROI analysis on the PFC region showed a tendency of greater electrical activity in high-performance participants relative to low-performance participants ($p = 0.076$).

4. Discussion

We applied a source localization technique to oscillatory electrical brain activity during a WM task to investigate the changes in cortical activity patterns depending on individual differences in memory capacity. The EEG source-localized results corresponded well with previous fMRI results [6, 7]. Instead of utilizing all the recall numbers, we selected a configuration of recall numbers 3–5, which had the lowest mean accuracy compared to other recall number configurations, to divide participants into performance groups. The intriguingly low accuracy for recall numbers 3–5 implies that participants have difficulty recalling the arrow direction in the middle of the sequence, and accuracy for these numbers is therefore an indicator of discrimination between correct and incorrect WM recall. We revealed a spectrum of localized activity changes associated with the performance in the WM task, which is closely related to individual WM capacity. Our results showed that an extensive network of cortical regions was activated in the high-performance group to accomplish successful memory encoding. This finding is in line with recent findings [16, 17], which also highlight a close coordination among different cortices to support mnemonic representations. A similar pattern was not observed in the low-performance group.

Previous reports [18, 19] have shown that optimal WM performance is closely related to selective attention. Selective attention helps prioritize salient information and refine the information for subsequent memory encoding, and contributes to the individual differences in memory capacity. In this study, concurrent cortical activations were found in the premotor cortex and dlPFC of the participants with higher recall accuracy. The premotor cortex is responsible for visuospatial attention (right BA 6), while the dlPFC is responsible for the selection of content-dependent, rule-based responses [20]. We inter-

![Fig. 5](image)

**Fig. 5** T-value map shows areas where cortical activity corresponding to the oscillatory EEG activity in the alpha band (8–13 Hz) is more enhanced in the high-performance than in the low-performance group.

<table>
<thead>
<tr>
<th>MNI coordinates (mm)</th>
<th>Voxel size</th>
<th>Cortical regions</th>
<th>Brodmann areas (L: left, R: right)</th>
</tr>
</thead>
<tbody>
<tr>
<td>−10 −100</td>
<td>0</td>
<td>1610 Secondary visual cortex</td>
<td>L18</td>
</tr>
<tr>
<td>16 −56 68</td>
<td>473</td>
<td>Somatosensory association cortex</td>
<td>R7</td>
</tr>
<tr>
<td>54 −20 −4</td>
<td>27</td>
<td>Superior temporal gyrus</td>
<td>R22</td>
</tr>
<tr>
<td>52 −22 −12</td>
<td>21</td>
<td>Middle temporal gyrus</td>
<td>R21</td>
</tr>
</tbody>
</table>

**Table 3** Summary of significantly activated foci showing more enhanced activity in the high-performance than in the low-performance group (two-sample t-test).

<table>
<thead>
<tr>
<th>MNI coordinates (mm)</th>
<th>Voxel size</th>
<th>Cortical regions</th>
<th>Brodmann areas (L: left, R: right)</th>
</tr>
</thead>
<tbody>
<tr>
<td>40 −74 0</td>
<td>58</td>
<td>Associative visual cortex</td>
<td>R19</td>
</tr>
<tr>
<td>50 −72 −2</td>
<td>40</td>
<td>Fusiform gyrus</td>
<td>R37</td>
</tr>
</tbody>
</table>
interpret the simultaneous activations in both the dIPFC and premotor cortex as a signature of successful interaction between attention and memory, which is strategically linked to the ability of exercising strong top-down control over new memory encoding [12] in posterior regions. Another study [22] showed that the strength of top-down signals originating from the dIPFC would partly affect individual memory capacity and subsequently determine the precision of memory management.

We observed strong engagement of the visual associative cortices but not of the prefrontal cortices when comparing high-performance to low-performance participants using a two-sample t-test. The lack of statistically significant activity in the PFCs may be attributed to the lower statistical power due to small number of participants in the subgroups. Meanwhile, enhanced activities in the right parieto-occipital region confirmed strong engagement of the visual associative cortices during visual WM-task encoding to maintain attention to the salient visual stimuli [23]. The role of the parieto-occipital region includes optimizing attentional modulation in visual search based on relevant features and influencing target selection [24]. Eventually, these observations suggest a direct relationship between performance accuracy and the amount of interaction within parieto-occipital regions. In addition, activations detected in the angular gyrus in high-performance participants are likely to play a critical role in relaying signal transmission between the frontal and posterior cortices. The angular gyrus acts as an interchange to connect top-down signals from the PFC and multisensory inputs from the visual processing cortices [25].

The work has several limitations. Although the present EEG source-localization results for the whole encoding period showed good accordance with previous fMRI results, more temporally specific analyses such as exploring regional activities for periods of each recall number could be performed to further utilize the good temporal resolution of EEG. Functional or effective connectivity analyses would also enhance the significance of this work to confirm our hypothesis that the frontoparietal cortical network may determine the working memory performance.

5. Conclusion

The present findings reveal a markedly complex, objective-driven, cognitive modulation that takes place beneath a seemingly straightforward cognitive process. Our claim is strengthened by the lack of significant activations in the prefrontal cortices in the low-performance group, which is attributed to less persistent top-down control, most probably due to the inappropriate allocation of selective attention [5] to simultaneously acquire new items and maintain the collected items. Future studies would employ time-sliced epochs combined with connectivity analysis to explore the temporal and functional relationships of the cortical activations identified in the present study.

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References


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