Neural Mechanisms of Memory Enhancement and Impairment Induced by Visual Statistical Learning

Sachio Otsuka and Jun Saiki

Abstract

Prior research has reported that the medial temporal, parietal, and frontal brain regions are associated with visual statistical learning (VSL). However, the neural mechanisms involved in both memory enhancement and impairment induced by VSL remain unknown. In this study, we examined this issue using event-related fMRI. fMRI data from the familiarization scan showed a difference in the activation level of the superior frontal gyrus (SFG) between structured triplets, where three objects appeared in the same order, and pseudorandom triplets. More importantly, the precentral gyrus and paracentral lobule responded more strongly to Old Turkic letters inserted into the structured triplets than to those inserted into the random triplets, at the end of the familiarization scan. Furthermore, fMRI data from the recognition memory test scan, where participants were asked to decide whether the objects or letters shown were old (presented during familiarization scan) or new, indicated that the middle frontal gyrus and SFG responded more strongly to objects from the structured triplets than to those from the random triplets, which overlapped with the brain regions associated with VSL. In contrast, the response of the lingual gyrus, superior temporal gyrus, and cuneus was weaker to letters inserted into the structured triplets than to those inserted into the random triplets, which did not overlap with the brain regions associated with observing the letters during the familiarization scan. These findings suggest that different brain regions are involved in memory enhancement and impairment induced by VSL.

INTRODUCTION

It is important for human beings to recognize visual objects in natural environments, to make associations between them, and to memorize these associations because this type of learning can help our behavior in a subsequent similar situation. For example, if we see a coffee shop, then a house with a green roof, and then a gas station every day on the way to work or school, after a while, when we see the coffee shop on the way to work or school, we expect to see the house with a green roof subsequently. Moreover, when we encounter a truck parked on a street (which is not usually parked there) between the coffee shop and the house with a green roof, we can immediately identify this strange object and recognize it as something that we do not usually see. In our environment, visual cognition and memory, as described above, are thought to be supported by visual statistical learning (VSL; cf. Jun & Chong, 2018). VSL is defined as the extraction of regularities embedded in a visual stream of stimuli (e.g., Otsuka & Saiki, 2016; Brady & Oliva, 2008; Turk-Browne, Isola, Scholl, & Treat, 2008; Fiser & Aslin, 2002).

Recently, we examined whether VSL enhances the memory of objects with statistical regularities, in addition to impairing the memory of items that break regularities (Otsuka & Saiki, 2016). Sufficient attention to items during encoding is critical for subsequent recognition memory performance (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996). In addition, Zhao, Al-Aidroos, and Turk-Browne (2013) demonstrated that attention is captured by statistical learning. In other words, visual attention is gradually directed to features and locations of objects with statistical regularities without conscious awareness. Furthermore, Campbell, Zimerman, Healey, Lee, and Hasher (2012) showed that young people learned the regularities of attended triplets, but not those of unattended triplets. On the basis of these previous findings, Otsuka and Saiki (2016) hypothesized that VSL enhances the memory of objects with statistical regularities but impairs the memory of items that disrupt regularities. According to this hypothesis, our previous results showed that objects of structured triplets were more often remembered than those of random triplets and that letters inserted into structured triplets were less frequently remembered than those inserted into random triplets.

In this study, we aimed to explore the neural mechanisms of both memory enhancement and memory impairment induced by VSL, using event-related fMRI. In the past decade, some studies identified the brain regions involved in VSL. Turk-Browne et al. showed that VSL modulates the brain activity in the right hippocampus and right caudate (Turk-Browne, Scholl, Chun, & Johnson, 2009) and that predictive and predicted items induced the brain activity in the anterior hippocampus and left inferior parietal lobule (IPL), respectively.
In addition, Schapiro, Rogers, Cordova, Turk-Browne, and Botvinick (2013) demonstrated that creation of a community structure of mutually predictive visual events activated the left inferior frontal gyrus (IFG), insula, anterior temporal lobe, and superior temporal gyrus (STG). According to these previous studies, we can predict that the medial temporal regions including the hippocampus, parietal regions including the IPL, and frontal regions including the IFG could be involved in VSL and VSL-induced memory enhancement (i.e., the retrieval of objects with statistical regularities). Especially, considering the previous findings of Turk-Browne et al. (2010), we hypothesized that the anterior hippocampus and left IPL could be respectively involved in the processing of predictive and predicted items during VSL.

Apart from memory impairment induced by VSL, many previous studies delineated the brain regions related to so-called inhibition. Yaple and Arsalidou (2017) conducted a meta-analysis of 14 fMRI studies that examined negative priming (e.g., Tipper & Driver, 1988; Tipper, 1985) and suggested that the right middle frontal gyrus (MFG), left STG, and ACC are important for inhibition. Moreover, Stroop interference (Stroop, 1935) and intentional suppression (e.g., Kim & Yi, 2013; Anderson & Green, 2001) elicited the activation of ACC (e.g., Anderson et al., 2004; Pardo, Pardo, Janer, & Raichle, 1990). If processing of items that disrupt the statistical regularities and memory impairment induced by VSL is supported by inhibition mechanisms such as negative priming, Stroop interference, and intentional suppression, we should be able to observe activations in the IPL, MFG, STG, and ACC. However, the brain mechanisms that underpin memory impairment induced by VSL remain unclear. In this study, we addressed this unresolved problem.

In addition, we examined the relationships between (1) memory enhancement of objects of the structured triplets during the recognition memory test scan and VSL during the familiarization scan and (2) memory impairment of letters inserted into the structured triplets and processing of letters that disrupt the statistical regularities. Whereas the abovementioned studies (Turk-Browne et al., 2009, 2010) focused on brain regions related to the familiarization phase of the VSL paradigm, here, we first explored regions activated during a familiarization scan overlapping with those activated during a recognition memory test scan using conjunction analysis. This study should suggest the neural mechanisms of memory enhancement and impairment induced by VSL, that is, visual cognition and memory in our daily life.

METHODS
Participants
Thirty-five Japanese graduate and undergraduate students from Kyoto University (19 men and 16 women, age range = 20–28 years) participated in this experiment in exchange for a book coupon worth 5000 Japanese yen. All participants were right-handed, and all of them had normal or corrected-to-normal visual acuity (according to self-report). Data from three participants (three men) were not used in the following analyses because they did not follow our instruction during the familiarization scan: Two participants continued to press the button, and the remaining one fell asleep. All participants provided written informed consent. All experimental protocols were approved by the institutional review board of Doshisha University.

We conducted a priori power analysis (effect size: $d = 0.5$, $\alpha = .05$, and power = .80) for reference, using G*Power 3 (Faul, Erdfelder, Lang, & Buchner, 2007). This analysis suggested a sample size of 34. More importantly, we determined our sample size to counterbalance the stimuli across participants. As described in the following section, we created 16 stimulus lists.

Stimuli and Apparatus
We selected 24 objects with properties described by Endo, Saiki, Nakao, and Saito (2005). Half of the objects were used in the familiarization scan as four structured triplets, and the remaining objects were used as four pseudorandom triplets. Furthermore, we selected 24 Old Turkic letters and inserted them into both the structured and random triplets that appeared in the last part of the familiarization scan. In addition, we used 24 additional objects and 24 Turkic letters as nontarget items in the recognition memory scan. These stimuli were presented in white on a black background. We prepared 16 stimulus lists to counterbalance objects and letters across participants. For a localization scan, we selected 12 line drawings (apple, car, carrot, chair, dog, eagle, fly, gun, leg, piano, spoon, and window) as described by Snodgrass and Vanderwart (1980), 12 meaningful word stimuli written in Japanese katakana (“インク,” “カラス,” “サクラ,” “ミカン,” “スペークル,” “ミルク,” “レタス,” “サカナ,” “ハサミ,” “ミカン,” “クルマ,” and “トイレ”) as described by Chihara and Tsujimura (1985), and 12 faces (six male faces and six female faces) as described by Matsumoto and Ekman (1988).

Visual stimuli were presented on a screen at the back of the scanner bore. Participants observed them using a mirror attached to the head coil. This experiment was run on a Windows computer (Toshiba Dynabook TB85/N5), controlled by MATLAB (The MathWorks, Inc.) and the Psychophysics Toolbox (Kleiner et al., 2007; Brainard, 1997; Pelli, 1997). Behavioral responses were collected using an MRI-compatible fiber-optic button box.

Procedure
The experiment consisted of three scans: familiarization, recognition memory test, and localization scans. In the
familiarization scan consisting of two runs, with 24 objects, we prepared a visual stream containing 288 objects. The stimuli were presented individually for 800 msec each, separated by a randomly selected ISI of 1200, 3200, or 5200 msec (1200 msec: 50.00%; 3200 msec: 33.33%; 5200 msec: 16.67%). This procedure prevented the participants from predicting trial onsets and allowed statistical separation of BOLD responses in the following analysis (Turk-Browne et al., 2010).

Half of the sequences showed four triplets made from 12 objects that were consistently presented in the same order in the structured condition (e.g., ABC, DEF, GHI, and JKL). Each object within a list was assigned to a unique position within one of four triplets across participants. The other half of the sequences were made from four pseudorandom triplets. To hold the same positional structure as in the structured triplets, we assigned the remaining 12 objects to one of four positions in the random triplets (cf. Turk-Browne et al., 2009). More specifically, each object was presented only in positions A'-D'-G'-J', B'-E'-H'-K', or C'-F'-I'-L'. Structured and random triplets were presented in a random order with the following constraint: No triplet could be repeated sequentially (e.g., ABC-ABC). In addition, to examine the neural basis of impaired memory for items that disrupted the regularities of structured triplets, 24 Turkic letters were inserted into both the structured and random triplets in the last part of the familiarization scan (Sets 10–12). These letters appeared between the second and third objects in each structured and random triplet. Thus, participants observed a visual stream of 312 items (Figure 1; 288 objects from sequences, and 24 letters inserted into structured and random triplets). In the familiarization scan, participants were required to detect jiggling objects, which were moving to the left and right of a fixation dot, with their right index finger as quickly and accurately as possible. Objects randomly jiggled six times in each run. Participants were never notified that there was any structure in the visual stream of objects. In addition, in each familiarization run, there were six blank trials in which only the fixation dot was presented throughout the duration of 6000 msec.

After the familiarization scan, participants took a surprise recognition memory test. The recognition memory scan was separated into two runs, each consisting of either objects or Turkic letters. Each run contained 48 trials plus eight filler trials (four trials at the beginning and four trials at the end). In one half of the 48 trials, items presented in the familiarization scan appeared, and in the other half, new items that did not appear during the familiarization scan were presented. In each trial, participants observed a test item for 2000 msec and judged whether it had appeared in the familiarization scan by pressing the corresponding key (“index finger” for old and “middle finger” for new). ISIs were randomly selected from 2000, 4000, or 6000 msec (2000 msec: 50.00%; 4000 msec: 33.33%; 6000 msec: 16.67%). In each recognition memory run, there were 12 blank trials in which only the fixation dot was presented throughout the duration of 6000 msec. The order of runs was counterbalanced across participants. In this scan, we focused on the neural correlates of recognition memory for triplet items and inserted distractors.

To define the lateral occipital regions related to object recognition (Turk-Browne et al., 2009; Malach et al., 1995), participants took part in one run of a localizer scan. This localizer scan consisted of 18 blocks. In each block, 12 faces (six male faces and six female faces), 12 word

---

**Figure 1.** Examples from the familiarization scan. We used 24 objects as described by Endo et al. (2003). Rectangles with solid-line borders represent structured triplets (e.g., ABC), and those with dashed-line borders represent random triplets. Twenty-four Old Turkic letters were inserted into the structured and random triplets in the last part of the familiarization scan (Sets 10–12).
stimuli, or 12 line drawings were randomly presented. Each stimulus was presented for 800 msec with a 1200-msec ISI and 6-sec rest period, resulting in 30-sec blocks. There were eight blocks in each category. The three categories randomly alternated every 30 sec. Participants were required to detect a target stimulus that juggled in each block.

Finally, to examine whether participants learned the regularities of structured triplets during the familiarization scan, we required the participants to join a two-alternative forced-choice (2AFC) familiarity test outside the MRI scanner. In each test trial, two 3-object test sequences appeared at the center of the screen of a laptop. All objects were displayed for 500 msec, with an ISI of 500 msec. The two sequences were separated by an ISI of 1000 msec. One of the two test sequences was a triplet that appeared in the familiarization scan (ABC, DEF, GHI, and JKL). The other was a foil made from objects of three different triplets presented in the familiarization scan (AEL, DHL, GKC, and JBF). After the two test sequences were presented, participants were required to press either “1” or “2” to indicate whether the first or second test sequence seemed more familiar on the familiarization scan (i.e., a recognition memory test for the sequence presented during the familiarization scan). Each of the four triplets was tested eight times and was paired twice with each of the four foil sequences, for 32 test trials. As in most previous studies (e.g., Otsuka & Saiki, 2016; Brady & Oliva, 2008; Turk-Browne et al., 2008; Fiser & Aslin, 2002), participants’ performance in discriminating triplets from foils was used as a measure of VSL.

After the 2AFC familiarity test, the participants were asked whether they noticed if the stream had any structure during the familiarization scan. Specifically, participants were asked “Did you notice any patterns in the visual stream of objects in the first scan (i.e., the familiarization scan)?” and then “If so, please remember the patterns and choose the objects printed on the paper (such as those in Figure 1, but all 24 objects presented during the familiarization scan were printed) in serial order.”

fMRI Data Acquisition

We performed fMRI using a 3-T Siemens scanner (3.0-T MAGNETOM Verio) at Kokoro Research Center, Kyoto University. We acquired functional data with a T2*-weighted gradient-echo, EPI sequence (echo time = 25 msec, repetition time = 2000 msec, flip angle = 75°, matrix = 64 × 64, field of view = 224 mm, 3.5-mm thickness) with 34 axial slices. We acquired 258 volumes for the first half of familiarization run, 298 volumes for the second half of the familiarization run, 180 volumes for each recognition memory run, and 270 volumes for the localizer run. Structural images were acquired using a T1-weighted anatomical sequence (3-D magnetization prepared rapid gradient echo; echo time = 3.51 msec, repetition time = 2250 msec, flip angle = 9°, matrix = 256 × 256, 1.0 mm × 1.0 mm × 1.0 mm voxel size) after the familiarization scan.

Preprocessing

We performed pre-processing and statistical analyses using the SPM software (SPM 12, www.fil.ion.ucl.ac.uk) in MATLAB. Images were corrected for slice acquisition time, motion-corrected with realignment to the first volume, spatially normalized using the Montreal Neurological Institute (MNI) EPI template, and spatially smoothed using an 8-mm Gaussian kernel.

Data Analyses

Familiarization Scan

To examine the difference in neural responses with respect to the objects and letters between the structured and random sequences, we ran one general linear model analysis using SPM. Six event types for the objects (the first, second, and third objects from both the structured and random triplets) and two event types for the letters (letters inserted into the structured and random triplets) were then entered as separate regressors. We also included six regressors for each dimension of head motion as covariates of no interest (x translation = 0.166 mm, y translation = 0.397 mm, z translation = 0.436 mm, pitch = 0.004 rad, roll = 0.004 rad, yaw = 0.002 rad). These models estimated the contribution of each condition to the BOLD response in every voxel for each participant. We conducted a full-factorial design analysis for the brain data on objects in the second-level analysis, with the sequence type (structured vs. random) and object position (Position 1 vs. Position 2 vs. Position 3) as factors. In addition, the resulting parameter estimates (beta values) for letters inserted into the structured and random triplets in the last part of the familiarization scan were compared across participants using paired t tests. Voxels were judged to show a reliable difference in the familiarization scan if the F or t values reached a level of significance of cluster-level threshold of p < .05 corrected (the voxel-level threshold p < .001, uncorrected).

Recognition Memory Scan

Subsequently, to examine both how neural responses differed with recognition memory of objects and letters inserted into the structured and random triplets, we ran one additional general linear model analysis. Six event types for the items (objects from the structured triplets, objects from the random triplets, new objects, letters inserted into the structured triplets, letters inserted into the random triplets, and new letters) were then entered as separate regressors. It should be noted that images from trials with errors were not included in the first-level analysis of the fMRI data. Similar to the familiarization
scan, we included six regressors for each dimension of head motion (x translation = 0.015 mm, y translation = 0.136 mm, z translation = 0.119 mm, pitch = −0.002 rad, roll < 0.001 rad, yaw < 0.001 rad). These models estimated the contribution of each condition to the BOLD response in every voxel for each participant, and the resultant parameter estimates for each condition were compared using paired t tests. Voxels were judged to show a reliable difference between objects from the structured and random triplets or between letters inserted into the structured and random triplets in the recognition memory scan, using the same criteria as the familiarization scan.

Localizer Scan
To examine whether VSL, processing of letters that disrupt statistical regularities, and memory of both objects and letters modulated the brain activity in the regions selective to object recognition, we compared BOLD responses for objects from the structured and random sequences and those for letters inserted into the structured and random sequences, in both the familiarization and recognition memory scans, within a priori ROI from the localizer scan: the lateral occipital cortex (LOC). To localize the LOC for each participant, we contrasted images of line drawings with those of faces and word stimuli for each participant. The voxel with the highest t value in this region was used as the center of an 8-mm spherical ROI. We used the MarsBaR ROI toolbox to calculate percent signal changes (Brett, Anton, Valabregue, & Poline, 2002). We calculated percent signal changes separately in the left and right regions, and these data were collapsed.

RESULTS
Behavioral Results
In the familiarization scan, participants detected the jiggling objects with few errors (97.66%, SE = 1.56) and close to no false alarms. These results demonstrate that participants followed our instruction and observed the visual stream of objects. Subsequently, we conducted a one-sample t test to compare the proportion of triplets judged as familiar in the 2AFC familiarity test to chance level (50%). This analysis showed that triplets were successfully discriminated from foils (54.59%, SE = 1.80), t(31) = 2.55, p = .016, d = 0.45, suggesting that participants learned the regularities of structured triplets in the familiarization scan. After the experiment, none of the participants reported noticing regularities during the familiarization scan.

We calculated the proportion of recognition memory separately for objects and Turkic letters inserted into the sequences. First, a two-tailed paired t test was conducted on A for objects of structured and random triplets, which is a measure of discriminability (Zhang & Mueller, 2005). There was a significant difference between A for objects of the structured and random triplets (0.71, SE = 0.02 vs. 0.65, SE = 0.02), t(31) = 4.78, p < .001, d = 0.51. In addition, a two-tailed paired t test was performed on A for Turkic letters inserted into structured and random triplets. There was a significant difference between A for letters inserted into the structured and random triplets (0.59, SE = 0.03 vs. 0.66, SE = 0.02), t(31) = 2.60, p = .014, d = 0.48. In addition, memory enhancement for objects with statistical regularities (i.e., A of objects from the structured triplets − A of objects from the random triplets) was negatively correlated with memory impairment for letters that disrupt the regularities (i.e., A of letters inserted into the structured triplets − A of letters inserted into the random triplets; r = −0.363, p = .041; see Figure 2). These results are consistent with those of our previous study (Otsuka & Saiki, 2016), suggesting both memory enhancement for objects with regularities and memory impairment for letters that disrupt the regularities by statistical learning.

fMRI Results: Whole-brain Analysis
VSL (Predictive and Predicted Objects in the Familiarization Scan)
First, to explore how the neural responses differed with predictive and predicted objects from the structured triplets in the familiarization scan, we conducted a full-factorial analysis of the brain data of objects using sequence type (structured vs. random) and object position (Position 1 vs. Position 2 vs. Position 3) as factors. We observed significant main effects of the sequence type in the bilateral IPL (peak of mass in MINI coordinates in the right hemisphere: 45, 35, 5; p < .001 corrected; extent = 1092; peak F = 30.98; the left hemisphere: −48, 23, 20; p = .001 corrected; extent = 159; F = 17.25), left STG (−51, 17, −7; p = .041 corrected; extent = 73; F = 24.88), left insula (−54, −40, 20; p < .001 corrected; extent = 225; F = 20.98), left medial frontal gyrus (−6, 8, 47; p < .001 corrected; extent = 545; F = 20.44), and left MFG (−39, −1, 44; p = .047 corrected; extent = 70; F = 18.79). All these regions exhibited lower activation levels for the objects in the structured triplets than those in the random triplets. Conversely, the effect of object position was not significant in any region. In addition, we observed a significant interaction between sequence type and object position in the right superior frontal gyrus (SFG: 15, −10, 68; p < .001 corrected; extent = 217; F = 13.42). Subsequently, we conducted a two-way within-participants ANOVA on the data of percent signal changes in the right SFG. There was a significant interaction, F(2, 62) = 3.44, MSE = 0.002, p = .038, ηp² = .100, thereby indicating that the simple main effect of Sequence Type was significant in Position 2 (structured: 0.001, SE = 0.009; random: 0.032, SE = 0.005), F(1, 31) = 9.01, MSE = 0.002, p = .005, ηp² = .225, and in Position 3 (structured: −0.002, SE = 0.008;
Memory Enhancement of Objects from the Structured versus Random Triplets in the Recognition Memory Test Scan

We focused on the neural correlates of memory enhancement of objects during the recognition memory test scan to examine whether the brain regions involved in VSL were reactivated when recognizing the objects with statistical regularities. Objects from the structured triplets were contrasted with those from the random triplets. This contrast showed that the bilateral MFG (the right hemisphere: 27, 29, 47; \(p < .001\) corrected; extent = 634; peak \(t = 5.20\); the left hemisphere: \(-21, 20, 44; p = .006\) corrected; extent = 142; \(t = 5.09\)) and right SFG (12, 65, 20; \(p = .016\) corrected; extent = 111; \(t = 4.53\)) responded more strongly to objects from the structured triplets than those from the random triplets (see Table 2 and Figure 4A and B). These results suggest that the abovementioned regions are related to recognition memory of objects during VSL. More importantly, we observed more activations in the right SFG for objects from the structured triplets than for those from the random triplets during the recognition memory test scan.\(^2\)

Furthermore, to examine the relationship between behavioral memory performance and brain activity, we conducted the same whole-brain analysis with the differences between \(A\) of objects from the structured triplets and \(A\) of objects from the random triplets as covariates. The right IPL (39, −52, 47; \(p = .002\) corrected; extent = 173; \(t = 4.82\)) responded more strongly to objects from the structured triplets than to objects from the random triplets (see Table 2 and Figure 4A and B). These results suggest that the abovementioned regions are related to recognition memory of objects during VSL. More importantly, we observed more activations in the right SFG for objects from the structured triplets than for those from the random triplets during the recognition memory test scan.\(^2\)

Table 1. Results of the Familiarization Scan

<table>
<thead>
<tr>
<th>Region</th>
<th>Hemisphere</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Extent</th>
<th>Peak (F)</th>
<th>Peak (t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main effect of sequence type</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IFG</td>
<td>R</td>
<td>45</td>
<td>35</td>
<td>5</td>
<td>1092</td>
<td>30.98</td>
<td></td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>−48</td>
<td>23</td>
<td>20</td>
<td>159</td>
<td>17.25</td>
<td></td>
</tr>
<tr>
<td>STG</td>
<td>L</td>
<td>−51</td>
<td>17</td>
<td>−7</td>
<td>73</td>
<td>24.88</td>
<td></td>
</tr>
<tr>
<td>Insula</td>
<td>L</td>
<td>−54</td>
<td>−40</td>
<td>20</td>
<td>225</td>
<td>20.98</td>
<td></td>
</tr>
<tr>
<td>Medial frontal gyrus</td>
<td>L</td>
<td>−6</td>
<td>8</td>
<td>47</td>
<td>345</td>
<td>20.44</td>
<td></td>
</tr>
<tr>
<td>MFG</td>
<td>L</td>
<td>−39</td>
<td>−1</td>
<td>44</td>
<td>70</td>
<td>18.79</td>
<td></td>
</tr>
<tr>
<td>Interaction of sequence type and object position</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SFG</td>
<td>R</td>
<td>15</td>
<td>−10</td>
<td>68</td>
<td>217</td>
<td>13.42</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Results of the Recognition Memory Test Scan

<table>
<thead>
<tr>
<th>Region</th>
<th>Hemisphere</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Extent</th>
<th>Peak (F)</th>
<th>Peak (t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Letters inserted into the structured triplets &gt; letters inserted into the random triplets</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precentral gyrus</td>
<td>R</td>
<td>36</td>
<td>−13</td>
<td>50</td>
<td>231</td>
<td>4.82</td>
<td></td>
</tr>
<tr>
<td>Paracentral lobule</td>
<td>L</td>
<td>−9</td>
<td>−25</td>
<td>47</td>
<td>190</td>
<td>4.61</td>
<td></td>
</tr>
</tbody>
</table>

Regions activated during the familiarization scan. \(x/y/z\) indicates cluster center-of-gravity coordinates in MNI space, “Extent” indicates number of suprathreshold voxels in the cluster, and “Peak \(F\)” or “Peak \(t\)” indicates maximum statistic within the cluster. L = left; R = right.
t = 5.39) responded more strongly to objects from the structured triplets than to those from the random triplets.

**Inserted Letters That Disrupt the Statistical Regularities in the Familiarization Scan**

Subsequently, we contrasted letters inserted into the structured triplets with those inserted into the random triplets, to examine if and how neural responses differed with letters that disrupted the statistical regularities. The right precentral gyrus (36, −13, 50; p < .001 corrected; extent = 231; t = 4.82) and left paracentral lobule (−9, −25, 47; p = .001 corrected; extent = 190; t = 4.61) responded more strongly to letters inserted into the structured versus random triplets (see Table 1 and Figure 5A and B).

**Memory Impairment of Letters Inserted into the Structured versus Random Triplets in the Recognition Memory Test Scan**

Next, we contrasted letters inserted into the structured triplets with those inserted into the random triplets, to examine the neural correlates of memory impairment (deactivation) of letters during the recognition memory test scan. The responses of the left lingual gyrus (−15, −74, 2; p = .001 corrected; extent = 165; t = 5.54), bilateral STG (the right hemisphere: 66, −10, 5; p = .013 corrected; extent = 104; t = 5.34; the left hemisphere: −63, −19, 2; p = .002 corrected; extent = 158; t = 5.20), and right cuneus (12, −85, 17; p = .022 corrected; extent = 91; t = 4.37) were weaker to letters inserted into the structured triplets than to those inserted into the random triplets (see Table 2 and Figure 6A–C).

We conducted the same whole-brain analysis with the differences between A of letters inserted into the structured triplets and A of letters inserted into the random triplets as covariates. However, we did not find any reliable activations with the contrast of letters inserted into the structured triplets with those inserted into the random triplets.

**fMRI Results: ROI Analysis**

As described in the Methods section, we examined both the effect of VSL and memory of objects in the LOC in each participant using the localizer scan. Pertinent ROIs were found bilaterally in 26 participants. Two-way within-participants ANOVA with regard to percent signal changes during the familiarization scan showed that there was a significant interaction between Sequence Type and Object Position, F(2, 50) = 3.57, MSE = 0.006, p = .036, η^2 = .125), thereby indicating that the simple main effect of Sequence Type was significant in Position 2 (structured: 0.129, SE = 0.028; random: 0.185, SE = 0.028), F(1, 25) = 5.18, MSE = 0.008, p = .032, η^2 = .172, and in Position 3.

**Table 2. Results of the Recognition Memory Test Scan**

<table>
<thead>
<tr>
<th>Region</th>
<th>Hemisphere</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Extent</th>
<th>Peak t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Objects of the structured triplets &gt; objects of the random triplets</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MFG R</td>
<td>27</td>
<td>29</td>
<td>47</td>
<td>634</td>
<td>5.20</td>
<td></td>
</tr>
<tr>
<td>MFG L</td>
<td>−21</td>
<td>20</td>
<td>44</td>
<td>142</td>
<td>5.09</td>
<td></td>
</tr>
<tr>
<td>SFG R</td>
<td>12</td>
<td>65</td>
<td>20</td>
<td>111</td>
<td>4.53</td>
<td></td>
</tr>
<tr>
<td>SFG L</td>
<td>−63</td>
<td>−19</td>
<td>2</td>
<td>165</td>
<td>5.54</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Letters inserted into the structured triplets &lt; letters inserted into the random triplets</th>
<th>Hemisphere</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Extent</th>
<th>Peak t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lingual gyrus L</td>
<td>−15</td>
<td>−74</td>
<td>2</td>
<td>165</td>
<td>5.54</td>
<td></td>
</tr>
<tr>
<td>STG R</td>
<td>66</td>
<td>−10</td>
<td>5</td>
<td>104</td>
<td>5.34</td>
<td></td>
</tr>
<tr>
<td>Cuneus R</td>
<td>−63</td>
<td>−19</td>
<td>2</td>
<td>158</td>
<td>5.20</td>
<td></td>
</tr>
</tbody>
</table>

Regions activated during the recognition memory test scan. x/y/z indicates cluster center-of-gravity coordinates in MNI space, “Extent” indicates number of suprathreshold voxels in the cluster, and “Peak t” indicates maximum statistic within the cluster. L = left; R = right.
(structured: 0.144, \(SE = 0.033\); random: 0.195, \(SE = 0.053\)), \(F(1, 25) = 5.31, MSE = 0.006, p = .030, \eta^2_p = .175\), but not in Position 1 (structured: 0.205, \(SE = 0.036\); random: 0.188, \(SE = 0.024\); \(F < 1\)). In addition, we conducted a two-tailed paired \(t\) test on signal changes for letter stimuli presented at the end of the familiarization scan. There was a significant difference in percent signal changes between letters inserted into the structured (0.178, \(SE = 0.033\)) and random (0.269, \(SE = 0.032\)) triplets, \(t(25) = 2.90, p = .008, d = 0.54\). In addition, we performed a paired \(t\) test on signal changes in the recognition memory scan for Turkic letters inserted into the structured and random triplets. The signal changes were lower for the letters inserted into the structured triplets (0.074, \(SE = 0.040\)) than for those inserted into the random triplets (0.228, \(SE = 0.045\)), \(t(25) = 2.71, p = .012, d = 0.70\).

Subsequently, we examined both the effect of processing of inserted letters that disrupted regularities and memory of inserted letters in the LOC. First, we conducted a two-tailed paired \(t\) test on signal changes for letter stimuli presented at the end of the familiarization scan. There was a significant difference in percent signal changes between letters inserted into the structured (0.178, \(SE = 0.033\)) and random (0.269, \(SE = 0.032\)) triplets, \(t(25) = 2.90, p = .008, d = 0.54\). In addition, we performed a paired \(t\) test on signal changes in the recognition memory scan for Turkic letters inserted into the structured and random triplets. The signal changes were lower for the letters inserted into the structured triplets (0.074, \(SE = 0.040\)) than for those inserted into the random triplets (0.228, \(SE = 0.045\)), \(t(25) = 2.71, p = .012, d = 0.70\).
In addition, we examined the relationship between functional connectivity and percent signal changes in the LOC. There was a significant positive correlation between functional connectivity for objects with statistical regularities (i.e., A of objects from the structured triplets − A of objects from the random triplets) and the difference of signal changes of objects from the structured and random triplets (r = 0.406, p = 0.040). Moreover, we observed a marginally positive correlation between memory impairment for letters that disrupt the statistical regularities (i.e., A of letters inserted into the structured triplets − A of letters inserted into the random triplets) and the difference of signal changes of letters inserted into the structured and random triplets (r = 0.357, p = 0.073).

Finally, we conducted the following additional ROI analyses. First, to localize both the parahippocampal and fusiform gyri, which are selectively involved in the processing of objects and faces (e.g., Kanwisher, Chun, McDermott, & LeDed, 1996), we contrasted images of line drawings with those of faces for each participant. As a result, we localized the bilateral parahippocampal gyrus and right fusiform gyrus. Two-way within-participants ANOVA with regard to percent signal changes in the bilateral parahippocampal gyrus during the familiarization scan showed that there was a significant interaction between Sequence Type and Object Position, F(2, 50) = 6.99, MSE = 0.001, p = 0.002, ηp² = 0.219, thereby indicating that the simple main effect of Sequence Type was significant in Position 2 (structured: 0.014, SE = 0.011; random: 0.054, SE = 0.007), F(1, 25) = 12.39, MSE = 0.002, p = 0.002, ηp² = 0.331, and in Position 3 (structured: 0.012, SE = 0.010; random: 0.051, SE = 0.008), F(1, 25) = 17.68, MSE = 0.001, p < 0.001, ηp² = 0.414, but not in Position 1 (structured: 0.053, SE = 0.007; random: 0.049, SE = 0.006; F < 1). In contrast, we did not observe any significant effect in the right fusiform gyrus (Fs < 1). In addition, we conducted a two-tailed paired t test on signal changes in the bilateral parahippocampal gyrus for objects of structured and random triplets in the recognition memory scan. Signal changes were higher for the objects from the structured triplets (0.097, SE = 0.022) than for those from the random triplets (0.017, SE = 0.021), t(25) = 2.74, p = 0.011, d = 0.72. Furthermore, signal changes in the right fusiform gyrus were higher for the objects from the structured triplets (0.189, SE = 0.027) than for those from the random triplets (0.111, SE = 0.033), t(25) = 2.55, p = 0.017, d = 0.49. Taken together, we observed the same pattern of results in other brain regions related to object processing as those observed in the LOC, except for the right fusiform gyrus during VSL.

Figure 5. Results of whole-brain analysis for inserted letters in the familiarization scan. (A) The right precentral gyrus (36, −13, 50; p < 0.001 corrected; extent = 231; t = 4.82) exhibited stronger responses to letters inserted into the structured triplets than those inserted into the random triplets. (B) The left paracentral lobule (−9, 25, 47; p = .001 corrected; extent = 190; t = 4.61) exhibited stronger responses to letters inserted into the structured triplets than those inserted into the random triplets.

In addition, we conducted the two-tailed paired t test on signal changes in the right fusiform gyrus for objects of structured and random triplets in the recognition memory scan. Signal changes were higher for the objects from the structured triplets (0.189, SE = 0.027) than for those from the random triplets (0.111, SE = 0.033).
Second, we contrasted images of word stimuli with those of faces for each participant and localized the left middle occipital gyrus, which is sensitive to letter processing (e.g., Flowers et al., 2004), and the right fusiform gyrus, respectively. We examined both the effect of processing of inserted letters that disrupted regularities and memory for inserted letters in the above regions. First, we conducted a two-tailed paired \( t \) test on signal changes in the left middle occipital gyrus for letter stimuli presented at the end of the familiarization scan. There was a significant difference in percent signal changes between letters inserted into the structured (0.184, SE = 0.028)
and random (0.267, SE = 0.040) triplets, t(25) = 2.85, p = .009, d = 0.47. Conversely, we did not observe significant differences with regard to signal changes in the right fusiform gyrus, t(25) = 1.43, p = .164, d = 0.24. In addition, we performed a paired t-test on signal changes in the left middle occipital gyrus for letters inserted into the structured and random triplets in the recognition memory scan. The signal changes were lower for the letters inserted into the structured triplets (0.123, SE = 0.028) than for those inserted into the random triplets (0.213, SE = 0.031), t(25) = 2.38, p = .025, d = 0.58. Similar to the results of the familiarization scan, we did not observe significant differences with regard to signal changes in the right fusiform gyrus (t < 1). It has been shown that the fusiform gyrus is related to letter processing in the left hemisphere (e.g., Joseph, Gathers, & Piper, 2003). Taken together, we observed the same pattern of results in the letter-selective brain region as those observed in the LOC.

fMRI Results: Conjunction Analysis of Familiarization and Recognition Memory Test Scans

To examine the overlapping activated regions between VSL and memory enhancement or memory impairment for the objects and letters in recognition, we conducted a conjunction analysis of familiarization and recognition memory test scans for objects and letters, respectively. A conjunction analysis using SPM involves a test for the null hypothesis that not all contrasts are significant, corresponding to a logical “AND” (cf. Hofstetter, Achaibou, & Vuilleumier, 2012). Specifically, we conducted two whole-brain analyses: one that contrasts the objects from the structured triplets with those from the random triplets during the recognition memory test scan with the inclusive mask by the brain image of interaction between sequence type and object position during the familiarization scan; another one that contrasts letters inserted into the structured triplets with those inserted into the random triplets during the recognition memory test scan with the inclusive mask by the brain image of interaction between sequence type and object position during the familiarization scan. This analysis showed that the bilateral MFG (the right hemisphere: 37, 29, 37; p < .001 corrected; extent = 633; Z = 4.38; the left hemisphere: −21, 20, 44; p = .006 corrected; extent = 142; Z = 4.31) and right SFG (12, 65, 20; p = .017 corrected; extent = 110; Z = 3.94) were commonly activated (or deactivated) while learning statistical regularities and recognizing objects from structured sequences. In addition, the left lingual gyrus (−15, −76, 2; p = .001 corrected; extent = 165; Z = 4.58), bilateral STG (the right hemisphere: 66, −10, 5; p = .014 corrected; extent = 102; Z = 4.46; the left hemisphere: −63, −19, 2; p = .002 corrected; extent = 158; Z = 4.38), and right cuneus (12, −85, 17; p = .022 corrected; extent = 91; Z = 3.82) were commonly activated (or deactivated) while encountering letter stimuli that disrupted their regularities and recognition.

DISCUSSION

First, performance of the recognition memory test was higher for objects of the structured triplets than those of the random triplets. These results suggest that VSL enhances memory for objects alone. On the contrary, recognition memory performance was lower for letters inserted into the structured triplets than those inserted into the random triplets. These results indicated that recognition memory of items that disrupt regularities was impaired. The pattern of behavioral results was similar to that of our previous study (Otsuka & Saiki, 2016). Moreover, memory enhancement for objects with statistical regularities was negatively correlated with memory impairment for letters that disrupt the regularities. Our findings suggest that VSL both enhances and impairs memory, although there are individual differences in memory enhancement and impairment induced by VSL. However, it should be noted that a study with a sample size of 32 (at α = .05, effect size ρ = 0.3) has only 40% power of detecting the correlation.

Brain Regions Engaged in VSL (Predictive and Predicted Objects in the Familiarization Scan) and Memory Enhancement of Objects from the Structured Triplets

We observed that the bilateral IFG is engaged in learning the statistical regularities during the familiarization scan, which is partially comparable to the results of some previous studies on VSL (Karuza et al., 2013; Schapiro et al., 2013; Turk-Browne et al., 2010). Karuza et al. (2013) reported that the left IFG and the BG are related to statistical learning and word segmentation in an auditory speech stream. In addition, we observed a significant interaction in the right SFG, showing lower activation levels in Positions 2 and 3 of structured sequences than those of random sequences. The ROI analyses showed this pattern of results in the LOC and parahippocampal gyrus. It is notable that Turk-Browne et al. (2010) showed lower activation levels in the left IFG for the predicted items than for the unpaired items, which is consistent with our findings on attenuation effects. Besides statistical learning, Yi and Chun (2005) reported repetition attenuation in the parahippocampal place area for the attended scenes during repetition and suggested that attention plays an important role when neuronal activity is suppressed to processing of stimuli. Moreover, Choi and Henderson (2015) observed activity in the bilateral SFG while performing active vision tasks such as natural reading and scene viewing. In addition, Slotnick, Moo, Segal, and Hart (2003) reported activity in the right SFG related to item and source memory for
meaningless visual objects. Whether statistical learning shows repetition enhancement or repetition attenuation and regions that show enhancement or attenuation are open to discussion; however, it is possible that statistical learning consists of both learning the regularities, which leads to repetition enhancement, and perceptual processing of repeated stimuli with regularities, which leads to repetition attenuation.

In contrast, we did not observe a significant effect of Sequence Type in Position 1, which was inconsistent with our hypothesis that processing of predictive items would activate the anterior hippocampus (Turk-Browne et al., 2010). Furthermore, we did not observe repetition attenuation, which may not be comparable with the findings of Turk-Browne et al. (2010) who observed an anticipation effect in the STG and precentral gyrus with the contrast of unpaired images and first (predictive) images. It is possible that the right SFG is related to processing of predicted items in VSL but not of predictive items. It should be additionally noted that we did not replicate the activations in the hippocampus during VSL, different from the findings of the previous studies of VSL (Schapiro, Gregory, Landau, McCloskey, & Turk-Browne, 2014; Turk-Browne et al., 2009, 2010). Karuza et al. (2017) suggested that the hippocampal and parahippocampal regions are domain general in VSL regardless of the temporal or spatial information to be learned. Considering the activations in other brain regions including the bilateral IFG and left STG and the results of the ROI analyses, although the hippocampus is important for VSL (Schapiro et al., 2014), it is possible that VSL is supported by more than one brain region and that hippocampal activation is not essential for VSL. Further research will be needed to clarify this point.

Moreover, a whole-brain analysis of the data from the recognition memory test scan showed more activations for objects of the structured triplets than for those of the random triplets, in the MFG and the SFG, which are related to visual processing tasks such as reading and scene viewing (Choi & Henderson, 2015). In addition, a conjunction analysis to examine the overlapping regions between VSL and memory enhancement of objects in recognition showed the same region of activation (the MFG and SFG). Recently, it has been shown that activation of the right SFG is related to efficient response inhibition in a stop signal task and that this brain region plays a role in translating conflict anticipation to the control of impulsive response (Hu, Ide, Zhang, & Li, 2016). Considering the better behavioral performance of recognition memory and the enhancement of percept signal changes in the LOC, parahippocampal gyrus, and right fusiform gyrus for objects of the structured triplets than for those of the random triplets, our results suggest that the brain mechanisms including both the MFG and SFG should have the functions of not only visual processing but also memory representation for items enhanced by VSL and anticipation on statistical regularities.

### Brain Regions Engaged in Processing of Letters That Disrupt the Statistical Regularities

Subsequently, we focused on the brain activity related to processing of letters that disrupt the statistical regularities. We found more activations in the right precentral gyrus and left paracentral lobule, which are related to motor response and somatic sense (Lingnau & Downing, 2015; Graziano, Taylor, & Moore, 2002; Forss & Jousmäki, 1998; Sanes, Donoghue, Thangaraj, Edelman, & Warach, 1995; Schieber & Hibbard, 1993), when participants observed letters inserted into the structured triplets than when they observed those inserted into the random triplets. Unlike some previous studies discussed in the Introduction (Yaple & Arsalidou, 2017; Anderson et al., 2004; Pardo et al., 1990), we did not observe any brain activity related to negative priming, Stroop interference, and intentional memory suppression. Recently, Zhang et al. (2015) showed the presence of activity in the paracentral–cingulate cortical network when participants showed motor responses during not only “go successes” but also “stop errors” in the stop signal task. In our experiment, because participants did not respond to inserted letters, processing of items that disrupt the statistical regularities may be supported by the brain regions related to the intention of no response to them. Alternatively, considering the results from the ROI analyses with the LOC and left middle occipital gyrus that signal changes of letters inserted into the structured triplets were lower than those of letters inserted into the random triplets, processing of items that disrupt the regularities may involve regions related to attentional capture or attentional modulation for oddball stimuli (Fajkus, Míkl, Shaw, & Brázdíl, 2015; Stevens, Skudlarski, Gatenby, & Gore, 2000). Recently, Kim (2014) conducted a meta-analysis of 75 fMRI studies related to oddball stimulus processing and suggested that the precentral gyrus as well as ventral network components, including the TPJ and the anterior insula, are important to oddball effects.

### Brain Regions Engaged in Memory Impairment (Deactivation) of Letters Inserted into the Structured Triplets

Contrary to the abovementioned findings, we observed a lower activation level for letters inserted into the structured triplets than those inserted into the random triplets, in the lingual gyrus, STG, and cuneus, which are related to not only phonological processing of letters and words (Perrachione, Ghosh, Ostrovskaya, Gabrieli, & Kovelman, 2017; Wydell, Vuorinen, Helenius, & Salmelin, 2003; Simos et al., 2002) but also their visual processing (Muayqil, Davies-Thompson, & Barton, 2015; Mechelli, Humphreys, Mayall, Olson, & Price, 2000; Jernigan et al., 1998). The ROI analyses showed this pattern of results in the LOC and left middle occipital gyrus, which is consistent
with lower behavioral performance of recognition memory for letters inserted into the structured triplets than for those inserted into the random triplets. In addition, a conjunction analysis between processing of letters that disrupt the statistical regularities and memory impairment (deactivations) of letters inserted into the structured triplets showed the overlap of the lingual gyrus, STG, and cuneus. Thus, the brain mechanisms including the lingual gyrus, STG, and cuneus should have the functions of not only processing of letters and words but also memory representation for items impaired by statistical learning. Notably, these regions were not found in the whole-brain analysis of the data of familiarization scan. One possible reason for this discrepancy is that, whereas response inhibition or attentional capture for letters that disrupt the statistical regularities is supported by the precentral gyrus and paracentral lobule as described above, lower representation of letters induced by VSL is supported by the lingual gyrus, STG, and cuneus. Nonetheless, it is unclear that a conjunction analysis showed the same regions during the recognition memory test scan.

**Attentional Capture and Statistical Learning**

As described in the Introduction, Zhao et al. (2013) proposed that attention is spontaneously biased toward locations and features with statistical regularities. In addition, Otsuka and Saiki (2016) showed that memory for items with statistical regularities is enhanced and memory for items that disrupt the regularities is impaired by statistical learning. In this study, however, we could not clarify whether participant attention was directed toward the structured sequences compared with the random ones, as this would have required examination with an additional task. Although our previous study (Otsuka & Saiki, 2016) reported that RTs for a face–sex discrimination task were shorter after the presentation of structured triplets compared with random triplets, this issue will need to be further examined with an appropriate task.

More recently, Damsma, Taatgen, de Jong, and van Rijn (2020) reported that attention is not spontaneously biased toward locations and color features with rhythmic temporal regularities (i.e., the square was presented rhythmically with a given ISI), and attentional bias does not generalize to metric temporal regularity. They argued that the rhythmic temporal regularities presented in Damsma et al. (2020) might be less complex than those presented in Zhao et al. (2013), leading to a decrease in attentional bias with time. Future research will need to explore the extent to which memory enhancement and impairment for items induced by statistical learning generalize to our environment.

**Conclusion**

In the current study, participants showed a better memory performance for objects with statistical regularities; however, they showed worse memory performance for letters that disrupt the regularities. The brain regions (the middle and superior frontal regions) related to memory enhancement for objects from the structured sequences (i.e., retrieval of the context of objects) overlap with those engaged in VSL, whereas the brain regions (the lingual and superior temporal regions and the cuneus) related to memory impairment (deactivations) for letters that disrupt the regularities do not overlap with the regions (the precentral and paracentral regions) engaged in processing of the letters during statistical learning. These findings suggest that different brain regions related to memory enhancement and impairment induced by VSL should support visual cognition and memory in our daily life.

**Acknowledgments**

This work was supported by JSPS KAKENHI grants JP26780414, JP19H09736, and JP20H00107. This study was conducted using the MRI scanner and related facilities of Kokoro Research Center, Kyoto University.

Reprint requests should be sent to Sachio Otsuka, Graduate School of Human and Environmental Studies, Kyoto University, Kyoto 606-8501, Japan, or via e-mail: otsuka.sachio.8a@kyoto-u.ac.jp.

**Notes**

1. Similar to the familiarization and recognition memory scans, we included six regressors for each dimension of head motion (x translation = 0.007 mm, y translation = 0.144 mm, z translation = 0.084 mm, pitch < 0.001 rad, roll < 0.001 rad, yaw < 0.001 rad).

2. We conducted the same GLM analysis with RTs for each object in the recognition memory test as regressors (i.e., we excluded the effect of RTs on the BOLD responses). Similar to the results of whole-brain analysis in the Results section, the bilateral MFG (the right hemisphere: 27, 29, 47; p < .001 corrected; extent = 754; peak t = 5.21; the left hemisphere: −21, 20, 44; p = .005 corrected; extent = 147; t = 5.13) and right SFG (12, 65, 20; p = .027 corrected; extent = 96; t = 4.65) responded more strongly to objects from the structured triplets than to those from the random triplets. These results suggest that the above brain regions are related to recognition memory of objects during VSL, even excluding the effect of RTs.

3. We conducted the same GLM analysis with RTs for each letter in the recognition memory test as regressors. Although the responses of the left lingual gyrus (−15, −67, 2; p = .001 corrected; extent = 160; t = 5.51) and bilateral STG (the right hemisphere: 69, −13, 5; p = .006 corrected; extent = 124; t = 5.34; the left hemisphere: −63, −19, 2; p < .001 corrected; extent = 236; t = 5.50) were weaker to letters inserted into the structured triplets than to those inserted into the random triplets, we did not observe significant activations in the right cuneus. These results suggest that the right cuneus may not be related to memory impairment of letters that disrupt the statistical regularities.

4. We conducted the same ROI analyses including the right and left hemispheres as an additional factor. However, we did not observe any significant effect or interaction including this factor.


