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Successful encoding during natural reading is associated with fixation-related potentials and large-scale network deactivation

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34 **Abstract**

35 Reading literature (e.g., an entire book) is an enriching experience that qualitatively differs from
36 reading a single sentence; however, the brain dynamics of such context-dependent memory remains
37 unclear. This study aimed to elucidate mnemonic neural dynamics during natural reading of literature
38 by performing electroencephalogram (EEG) and functional magnetic resonance imaging (fMRI).
39 Brain activities of human participants recruited on campus were correlated with their subsequent
40 memory, which was quantified by semantic correlation between the read text and reports subsequently
41 written by them based on state of the art natural language processing procedures. The results of the
42 EEG data analysis showed a significant positive relationship between subsequent memory and
43 fixation-related EEG. Sentence-length and paragraph-length mnemonic processes were associated
44 with N1-P2 and P3 fixation-related potential (FRP) components and fixation-related theta-band (4-8
45 Hz) EEG power, respectively. In contrast, the results of fMRI analysis showed a significant negative
46 relationship between subsequent memory and blood-oxygenation-level dependent (BOLD) activation.
47 Sentence-length and paragraph-length mnemonic processes were associated with networks of regions
48 forming part of the salience network and the default mode network (DMN), respectively. Taken
49 together with the EEG results, these memory-related deactivations in the salience network and the
50 DMN were thought to reflect the reading of sentences characterized by low mnemonic load and the
51 suppression of task-irreverent thoughts, respectively. It was suggested that the context-dependent
52 mnemonic process during literature reading requires large-scale network deactivation, which might
53 reflect coordination of a range of voluntary processes during reading.

54

55 **Significance statement**

56 Context-dependent memory encoding during natural reading of literature was evaluated using
57 electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) based on a
58 subsequent memory paradigm. Subsequent memory was quantified by semantic correlation between
59 the read text and reports subsequently written by the participants, based on a recent natural language
60 processing procedure. Our results demonstrated a positive correlation between subsequent memory
61 and fixation-related EEG and a negative correlation with fMRI activity. Sentence-length and
62 paragraph-length processes were associated with regions belonging to the salience network and the
63 default mode network, respectively. This is the first demonstration that memory encoding during
64 literature reading is associated with large-scale network deactivations, which might reflect the
65 coordination of a range of voluntary processes during reading.

66

67 Introduction

68 Neural dynamics during memory encoding have been extensively investigated using the subsequent
69 memory paradigm (Brewer, 1998; Wagner, 1998), in which brain activity during encoding of items
70 that are subsequently remembered is compared to the activity during encoding of items that are
71 subsequently forgotten. Functional magnetic resonance imaging (fMRI) studies have demonstrated
72 that multiple brain regions, including the inferior frontal cortex and hippocampus, are activated during
73 successful memory encoding of words (Wagner, 1998), pictures (Brewer, 1998), and item-context
74 associations (Summerfield and Mangels, 2005) (also see the review by Kim (2011)). This activation is
75 termed the subsequent memory effect (SME). In contrast, the activation of distinct brain regions, such
76 as the anterior and posterior midline cortices, was also observed during unsuccessful encoding; an
77 effect termed the “subsequently forgotten effect” or “negative subsequent memory effect” (NSME)
78 (Otten and Rugg, 2001; Wagner and Davachi, 2001; Daselaar et al., 2004).

79
80 Electroencephalography (EEG) studies found that specific event-related potentials (ERPs) and brain
81 oscillations occur during the SME. Specifically, the P3 ERP component increases during successful
82 encoding of words (Klimesch et al., 2000). EEG theta (4-7 Hz) oscillations increased during successful
83 encoding of words (Klimesch et al., 1996), pictures (Osipova et al., 2006), and item-context binding
84 (Summerfield and Mangels, 2005) (also see review by Nyhus and Curran (2010)). However, opposite
85 effects, namely EEG theta decreases during successful encoding, have also been reported, suggesting
86 that the SME primarily reflects perceptual and cognitive processes engaged by the encoding tasks
87 (Hanslmayr and Staudigl, 2014). In these studies, relatively simple memory contents, such as single
88 words or item-location pairs have been used. Thus, it is of interest to investigate whether the same
89 neural dynamics is relevant for the encoding of a more natural form of memory consisting of
90 semantically richer and context-dependent material, for example the experience of reading literature.

91
92 Literature reading provides a good example of a semantically rich and context-dependent experience
93 for evaluating natural memory. The neural dynamics of reading has been extensively tested with
94 sequential presentation of words constituting sentences, using EEG (Kutas and Hillyard, 1980; Kutas
95 and Federmeier, 2000; Hagoort et al., 2004; Bastiaansen and Hagoort, 2006) and fMRI (Cutting et al.,
96 2006; Pallier et al., 2011). Moreover, the neural dynamics of narrative-level context have been
97 evaluated by EEG and fMRI studies (Ferstl and von Cramon, 2001; Xu et al., 2005; Hasson et al.,
98 2007; Yarkoni et al., 2008; Brennan, 2016). Some of these studies (Hasson et al., 2007; Yarkoni et al.,
99 2008) demonstrated a subsequent memory effect during narrative comprehension. However, the

100 examination of semantic contents after reading in these studies was based on a small number of
101 questions regarding the text, and these were found to be too abstract for capturing the entire semantics
102 of the text being read. Thus, the mnemonic process relevant to semantically rich content during reading
103 needs further elucidation.

104

105 Recently developed natural-language techniques are expected to be useful for quantifying the semantic
106 content of subsequent memory. One of these is “distributed semantic representation”, in which each
107 word is transformed to a vector consisting of intermediate semantic features. This technique is used to
108 perform text comparisons based on semantic correlation rather than the appearance of particular
109 keywords (Blei et al., 2003; Mikolov et al., 2013). The same technique has already been employed in
110 fMRI studies showing that intermediate features were associated with widely distributed cortical
111 regions (Mitchell et al., 2008; Huth et al., 2012). These studies are important in that they support the
112 plausibility of using intermediate features in the investigation of brain activities related to semantics.
113 Given the assumption that subsequent memory performance depends on a particular pattern of cortical
114 activation during encoding into long-term memory, these same intermediate features may be used for
115 the evaluation of subsequent memory of the texts.

116

117 In this study, we aimed to elucidate mnemonic neural dynamics during natural reading of literature
118 using EEG and fMRI measurements. Brain activity was analyzed by comparing the measurements
119 with content reports subsequently written by the participants based on a recently developed natural
120 language technique quantifying semantic correlations to body of text. EEG measurement was
121 combined with eye tracking to enable fixation-related potential (FRP) analysis during reading, by
122 which neural dynamics during free-viewing was assessed, while solving the problem of ocular artifact
123 contamination in EEG signals (Dimigen et al., 2011; Henderson et al., 2013). We specifically asked
124 the following questions: (1) What neural dynamics underlies memory encoding during natural reading
125 of literature? (2) What neural dynamics is associated with multi-scaled contextual processing during
126 reading of sentences and paragraphs?

127

128 **Methods**

129 We performed EEG and fMRI measurements separately during natural reading of identical texts. The
130 task procedures and statistical analyses in these two experiments were designed to be comparable.

131

132 **EEG Methods**

133 Subjects

134 Fifteen volunteers (2 female, 2 left-handed, native Japanese speakers; 20 to 34 years old (mean \pm s.d.:
135 22.5 ± 3.5 years old)) were recruited via poster advertisement at [Author University]. They had no
136 experience of neurological disorders or use of psychotropic medications and had normal visual acuity,
137 except that the eyes of 6 participants were corrected by spectacles and the eyes of 1 participant were
138 corrected by intraocular lenses. They were compensated \$25-30 for participating in the study; the exact
139 amount was prescribed by the city and depended on the school year of the participant in the [Author
140 University]. They provided written informed consent prior to participating in the experiment. The
141 study was approved by the Ethics Committee of the [Author University]. Data from the two left handed
142 volunteers were ultimately excluded from the analysis.

143

144 Stimuli

145 Four scientific essays written by Torahiko Terada, entitled “Eagle’s eye and olfaction”, “Rhythms of
146 poems”, “Physiological responses to seeing a movie”, and “A case study of a ghost” were used as
147 stimuli (Aozora Bunko, http://www.aozora.gr.jp/index_pages/person42.html). They were selected as
148 logical and non-emotional texts, suitable for high school students (unlike scientific articles). Each text
149 was modified to modern kana (Japanese syllabary spelling system) with a length of 1919.5 ± 77.6
150 words (2973.3 ± 137.3 characters, sentence length: 46.2 ± 22.9 words, paragraph length: 116.2 ± 82.4
151 words (mean \pm s.d.)). Their readability was measured as having a grade of “beyond high school (13)”
152 using a program based on a statistical language model, Obi-2 (Sato et al., 2008).

153

154 During reading, the essays were presented on a 21-inch monitor (Sony, CPD-G520), as a line of
155 segmented text with 40 characters, displayed as 985×24 pixels (subtending 27.9×0.74 degrees) in
156 white, on a black background. The single line presentation was used to restrict eye movements to
157 horizontal saccades or eye blinks (Dimigen et al., 2011). The participants voluntarily advanced to the
158 next line by pushing a button with the right thumb. Returning to a previous line was not allowed.

159

160 Procedure

161 Following the placement of EEG electrodes on the participants’ heads, they read the four essays in a
162 random order with rest intervals. During reading, the head position was stabilized by chin and forehead
163 rests. At the beginning of each reading session, the eye movement system was calibrated with a 9-point
164 grid. Following the reading session, the electrodes were removed, and the subjects washed their hair
165 to remove conducting gel (which lasted for approximately 15 min). The subjects were then seated at a

166 desk and wrote a summary of the content read (content report), as detailed as possible, following the
167 order in which the essays were read. During this procedure, the interval between essay encoding and
168 retrieval was approximately 30 min, and no explicit opportunities for rehearsing the essays were
169 included. Possible influence of rehearsals during the interval was thought to be reduced by the
170 separation of particular encoding and retrieval pairs using other essays tasks and the counter-balanced
171 order of the text presentation. Before the main experiment, subjects performed a training session with
172 a short essay (714 words) to familiarize themselves with the task.

173

174 Eye movement data acquisition

175 Eye movements were recorded binocularly with an infrared video-based eye tracker (EyeLink CL, SR
176 Research Systems) at a sampling rate of 250 Hz. During reading, saccades were detected by EyeLink
177 software using an eye-movement velocity threshold of 30 degrees/s, an acceleration threshold of 8000
178 degrees/s² and a saccadic threshold of 0.15 degrees. Data from the right eye were analyzed, and those
179 from the left eye were used only for validation. The following atypical fixations were discarded from
180 the analysis: fixations separated vertically by 48 pixels (2 characters) from the line, fixations with a
181 duration of < 50 ms or > 750 ms, fixations at the first or the last saccades during the reading of each
182 line, fixations for small (< 1 character) or large (> 20 character) saccades, and fixations shortly
183 preceding/following an eye blink (ranging from -500 to 1000 ms of blink onset).

184

185 EEG data acquisition and preprocessing

186 EEG and EOG data were acquired using Ag/AgCl electrodes with a BrainVision amplifier
187 (BrainProducts, Germany). Twenty-one electrodes were mounted on the scalp according to the
188 standard 10–20 system without Fp1 and Fp2. Four EOG electrodes were affixed to the left and right
189 outer eye canthi and above and below the right eye. EEG data (0.01-100 Hz bandpass, 500 Hz sampling
190 rate, impedance of the electrode 12.6 ± 11.6 k Ω (mean \pm s.d.)) were referenced to the FCz electrode
191 during measurements and re-referenced to the average signal recorded at electrodes placed on the two
192 earlobes for analysis.

193

194 Ocular artifacts were corrected by independent component analysis (Henderson et al., 2013). First, a
195 dataset dominantly including ocular artifacts, given by fixation-related data from -120 to 50 ms from
196 the fixation onset (20443 ± 11008 time points (481.8 ± 259.0 trials) (mean \pm s.d.) \times 26 electrodes, with
197 additional band-pass filtering between 1 Hz and 50 Hz), were collected and their independent
198 components were calculated by FastICA (Hyvärinen and Oja, 2000). Second, independent components

199 highly correlated to either horizontal, vertical, or radial EOGs (correlation coefficient of the entire time
200 course across trials > 0.15) were discarded, and the same separation matrix, calculated from the subset
201 of the data, was applied to the original data. By this procedure, 5.5 ± 2.3 components (mean \pm s.d.)
202 were discarded; this rejection rate was similar to the rate reported previously (Henderson et al., 2013).
203 Finally, the corrected EEG signals were filtered between 1 Hz and 40 Hz (using a zero-lag Butterworth
204 filter with -12 dB/octave roll-off) and down-sampled to 250 Hz to match the eye-movement data. EEG
205 and eye movement data were synchronized by a common trigger input from the stimulus computer.

206

207 Text data analysis

208 The analysis of the text data can be outlined as follows (Figure 1a). Each text consisting of an arbitrary
209 number of words was translated into a semantic vector consisting of intermediate semantic features
210 (Blei et al., 2003; Mikolov et al., 2013). Statistically, natural texts consist of approximately ten
211 thousand types of words and the collocation matrix appears sparse. Therefore the relationship between
212 the words (i.e., collocation matrix) can be computationally compressed and the dimension of the
213 compressed word relationship typically falls within the range of several hundred dimensions (Landauer
214 and Dumais, 1997). This compressed word relationship produces a word-to-vector map. When a text
215 is represented by the average of the word vectors relevant to the words in the text (“bag-of-words”),
216 the averaged vector, termed the “semantic vector,” captures the intermediate semantics of the text, in
217 a way that is robust against the influence of synonyms or rephrasing. For example, when two
218 intermediate semantic features represent the amount of “flying” or “vision” (Fig. 1a), a semantic vector
219 represents its semantics by the combined amounts of these semantic features, although in reality these
220 semantic features were automatically produced by the above algorithms to optimally cover natural
221 texts. The text that was read and the content reports subsequently written by the participants were
222 individually translated into semantic vectors, and their correlation was used as an index for semantic
223 text correlation evaluating the subsequent memory.

224

225 The detailed procedure applied in the text data analysis consisted of the following steps.

226 *Step 1.* The vector features of all words were computed from word-occurrence data within a large text
227 corpus (Balanced Corpus of Contemporary Written Japanese (BCCWJ) (Maekawa et al., 2014);
228 Library/Book sub-corpus (10,551 texts, 60,615 word types, fixed length of 1000 characters per text)
229 using the algorithm Word2Vec (Mikolov et al., 2013) (using the parameters: context window of 10
230 words, CBOW model, and negative word sampling of 15 words). For this process we used open source
231 code from <https://code.google.com/archive/p/word2vec/>.

232 *Step 2.* The words in every text were segmented into morphological units (“short-unit word”) using
 233 the Japanese morphological analyzer MeCab (<http://taku910.github.io/mecab/>) with the dictionary
 234 unidic-mecab (ver.2.1.3) (<https://ja.osdn.net/projects/unidic/>).

235 *Step 3.* Each open-class word (noun, verb, adverb, and adjective) within the text was represented by a
 236 100-dimensional vector \mathbf{w}_i , where i denotes word position in the given text.

237 *Step 4.* Three types of text correlation were calculated using sentence-length samples, paragraph-length
 238 samples, or the entire text. In the calculation, each text unit was represented by the average of the word

239 vector, $\mathbf{T}_T = \frac{1}{|T|} \sum_{i \in T} \mathbf{w}_i$, where \mathbf{w}_i is the i -th word vector in the text, and T is the set of word IDs

240 in the text. The correlation of a pair of texts represented by the semantic vectors \mathbf{T}_E and \mathbf{T}_R was
 241 determined by cosine similarity, $C(\mathbf{T}_E, \mathbf{T}_R) = \mathbf{T}_E \mathbf{T}_R / (|\mathbf{T}_E| |\mathbf{T}_R|)$, where the values range from -1 to 1,
 242 0 indicates an independent text pair, and 1 indicates an identical text pair.

243 *Step 5.* The correlation between the entire text read and the content report was termed the “performance”
 244 and used as a quality index for the individual content reports. To clarify whether the content reports
 245 specifically reflected the corresponding texts, surrogate text correlations, calculated as the average of
 246 correlations between the content report and non-corresponding texts, were additionally computed. The
 247 feature dimension (100) was determined to maximize the difference between the text read-content
 248 report correlation and the surrogate text correlations.

249 *Step 6.* In the following subsequent memory analysis, each sentence or paragraph of the text read was
 250 compared with the entire content report to identify which part of the text was reflected in the content
 251 report. The sentence-length correlations changed quickly as a function of word position, and
 252 paragraph-length correlations slowly because the former reflected the appearance of specific sentences
 253 while the latter reflected the appearance of abstract themes governing several sentences forming a
 254 paragraph. In the current analysis, text correlation was not highly sensitive to variation of word length
 255 in sentences or paragraph (i.e., results with fixed-length text correlations using the averaged sentence-
 256 or paragraph-length were fundamentally unchanged from the current results; data were partially shown
 257 in [SfN abstract shown by Author]), thus the influence was not corrected.

258

259 EEG data analysis

260 The corrected EEG signals were analyzed in terms of FRPs and fixation-related time-frequency power
 261 as follows. First, the corrected EEG signals were segmented from -500 to 1000 ms from the fixation
 262 onset given by the eye movement data. Segments including data points within a limit of $\pm 80 \mu\text{V}$ were
 263 used. Second, the influence of overlapped event-related potentials from neighboring fixations was

264 reduced by subtracting an estimated FRP calculated from de-convolution by the use of the Adjacent
265 Response Technique (Woldorff, 1993). Third, fixation-related time-frequency EEG power was
266 calculated using complex Morlet wavelet transformation (width = 5), where 19 frequency bands were
267 determined on a logarithmic scale ($2^{(1, 1.25, \dots, 5.5)}$ Hz) and split into four distinct bands, 4-7 Hz
268 (theta), 8-12 Hz (alpha), 14-28 Hz (beta), and 30-48 Hz (gamma). The baseline for each power was
269 subtracted; the baseline was calculated from the period within -300 to -100 ms from the fixation onset.
270 Finally, the time-frequency EEG power at time t and frequency f , $P(t, f)$, was compared with the
271 text correlation between the part of the text read at eye fixation and the content report. Two text
272 correlations, one at sentence-length and another at paragraph-length, C_s and C_p , were used in the
273 analysis. The time-frequency power was analyzed by multiple regression using the two text
274 correlations, as:

275

$$276 \quad P(t, f) = b_0 + b_s C'_s + b_p C'_p,$$

277

278 where C'_s and C'_p are the sentence-length and paragraph-length text correlations with a
279 modification of Gram-Schmidt orthogonalization. The regression coefficients b_s and b_p were
280 calculated separately for each electrode, each time point and each frequency band, and then integrated
281 across all subjects using the t -statistic. Multiple comparisons in the t -tests were corrected using the
282 nonparametric clustering permutation test (Maris and Oostenveld, 2007) with 4000 shuffled data sets,
283 in which the statistical threshold was provided by a single procedure taking into account the electrodes,
284 time, and frequency simultaneously. FRPs were also analyzed using the identical regression analysis,
285 where the regression coefficients were calculated separately for each electrode and each time point and
286 then integrated across all subjects using the t -statistic. Additionally, to quantify the potential
287 contribution of ocular artifact residuals in the corrected EEG, saccade size and fixation duration were
288 analyzed using the same type of regression analysis.

289

290 fMRI Methods

291 Subjects

292 Nineteen volunteers (10 female, all right-handed, native Japanese speakers; aged from 21 to 29 years
293 old (mean \pm s.d.: 23.9 ± 2.5 years old)) were recruited via poster advertisement at [Author University].
294 They had no experience of neurological disorders or use of psychotropic medications and had normal
295 visual acuity, except that the eyes of 13 participants were corrected by spectacles. They were

296 compensated \$65 for participating in the study. Written informed consent was provided prior to
297 participating in the experiment. The experimental protocol was approved by the ethics committee at
298 the [Author University]. Data from two volunteers were excluded from the analysis because of low
299 memory performance.

300

301 Procedure

302 The procedure was as described above for the EEG experiment. The participants read the two essays
303 at a natural pace within an MR scanner for 10 min. The texts were two out of four essays used in the
304 EEG experiment, the titles of which were “Eagle’s eye and olfaction” and “Physiological responses to
305 seeing a movie.” While reading, two lines of the text (60 characters) were displayed, with the
306 participant voluntarily advancing to the next page by pressing a button (the essays consisted of 50 and
307 54 pages, respectively). To have page transition intervals longer than the timescale of hemodynamic
308 response (for stable regressing out of the influence of page transition and button pressing in the
309 following analysis), the number of characters in a page was changed to be larger than that of the EEG
310 experiment. After the two texts were read, a 5-min structural scan was performed. Following structural
311 scanning, the participants sat at a desk outside the scanner and wrote two content reports within 15
312 min, following the order in which the essays were read in as much detail as possible. In this procedure,
313 the interval between essay encoding and essay retrieval was approximately 20 min.

314

315 fMRI data acquisition and preprocessing

316 During reading, blood oxygenation sensitive echoplanar images (EPI) were acquired using the 3T MR
317 scanner (Magnetom Verio, Siemens, Erlangen, Germany) under the following conditions: repetition
318 time = 2 s, echo time = 30 ms, flip angle = 80°, field of view = 192 mm, in-plane resolution = 64 × 64,
319 30 axial slices, slice thickness = 5 mm. One session lasted for ≤ 10 min (297 scans) as defined by the
320 reading time for each essay. Two sessions were performed, one for each essays. After reading, a T1-
321 weighted anatomical volume was acquired.

322

323 We used SPM8 software (Wellcome Department of Cognitive Neurology, London, UK, URL:
324 www.fil.ion.ucl.ac.uk/spm) for image preprocessing and voxel-based statistical analysis. The initial
325 five scans in each session were discarded from the analysis to eliminate magnetic saturation effects.
326 The remaining EPIs (≤ 292 scans × 2 sessions) were mapped to the first image volume for each
327 participant to correct for head motion. The slice timing was corrected with respect to the middle slice
328 to remove the time delay of scanning the entire brain. The individual EPIs were normalized to a

329 standard brain by applying the parameters estimated by matching the T1 anatomical image to the
330 stereotactic image in Montreal Neurological Institute coordinates. The EPIs were then smoothed with
331 an 8-mm full-width at half-maximum Gaussian kernel.

332

333 **fMRI analysis:**

334 A voxel-based statistical analysis was performed on the preprocessed EPIs. The blood-oxygenation-
335 level dependent (BOLD) responses were evaluated using a general linear model including regressors
336 of interest, which were the sentence-length and paragraph-length text correlations between the text
337 read and the content report. The text correlations were calculated identically to those in the EEG
338 analysis, except for one parameter in Word2Vec (a context window parameter was changed from 10 to
339 15 words to maximize the difference between the correlations of the content report with the text read
340 and the correlations with non-corresponding texts). In contrast to the fixation-related EEG analysis,
341 the text correlation was associated with the BOLD signals at each scanning time, in which many eye
342 fixations were included. To identify neural mechanisms underlying text correlations, we hypothesized
343 an expected BOLD response by convolving the canonical hemodynamic response function with the
344 text correlations for each participant and session. The model additionally included the time taken to
345 press the button and six motion regressors obtained from the registration process.

346

347 Before performing the regression analysis, low-frequency confounding effects were removed using a
348 high-pass filter with a 120 s cut-off period, and serial correlations among the scans were estimated
349 using an autoregressive model [AR(1)] to remove the high-frequency noise contaminating the EPI time
350 series. The parameter estimates were computed for each subject using a fixed-effects model and then
351 taken into the group analysis using a random-effects model of a t-statistic (uncorrected $p < 0.001$,
352 cluster-wise FDR ($p < 0.05$)).

353

354 **Results**

355 **Behavioral results**

356 The 13 participants who underwent EEG measurements took a mean time of 7.4 min (s.d., 2.4 min) to
357 read each of four essays and write four content reports with a mean length of 205.8 words (s.d., 130.8
358 words) in a mean time of 12.0 min (s.d., 6.4 min). The performance (the entire text correlation between
359 the content reports and the text read) was calculated as 0.80 ± 0.05 (mean \pm s.d.) which was
360 significantly larger than the surrogate text correlation (0.61 ± 0.06) (paired t-test, $t(12) = 102.7$, $p <$
361 0.001). It was therefore clearly demonstrated that the participants properly described the content of the

362 text read (Figure 1b).

363

364 In the fMRI experiment, all 17 participants read each of the two essays during a mean period of 8.2
365 min (s.d., 1.9 min) (246.4 ± 55.8 volumes) and wrote content reports having a mean length of 281.3
366 words (s.d., 85.5 words) within 10 min. The memory performance was calculated as 0.77 ± 0.06 (mean
367 \pm s.d.) (t-statistic comparing the text correlation to surrogate text correlation (0.44 ± 0.13); $t(16) =$
368 52.5 , $p < 0.001$). The difference between the memory performance of fMRI participants and that of
369 EEG participants was not significant ($t(28) = 1.74$, $p = 0.09$), suggesting that cognitive processes in
370 the fMRI- versus EEG- participants were comparable.

371

372 EEG results

373 After rejecting atypical saccades (defined by atypical fixation duration or saccade size or too small
374 separation from blinks), a mean of 481.8 fixations (s.d., 259.0 fixations) were analyzed for each text
375 and each participant. The mean duration of fixation was 287.5 ms (s.d., 92.7 ms), and the mean saccade
376 size was 2.1 characters (s.d., 4.7 characters). These values agreed with the typical values recorded
377 during reading in English (Rayner, 1998).

378

379 Figure 2a shows FRPs of the grand averaged signal. The red and blue plots show FRPs related to higher
380 and lower regression coefficients for the sentence-length comparison, where higher and lower
381 regression coefficients were defined by a median split of the regression coefficients. The shape of the
382 FRPs appeared similarly to those reported during reading by Dimigen et al. (2011). In the FRP analysis,
383 there were 65 clusters of (electrode, time)-samples (60 positive and 5 negative) showing the sentence-
384 length subsequent memory effect and 45 clusters of samples (19 positive and 26 negative) showing
385 paragraph-length effects. The two positive clusters showing a sentence-length effect, in the time
386 periods 0.10–0.21 s ($p = 0.018$) and 0.38–0.48 s ($p = 0.025$), had Monte Carlo p-values that were less
387 than 0.025 (Figure 2a). As also shown in Figure 2b, both clusters broadly distributed over the scalp,
388 while the former and the latter appeared in the left central area and in the frontal area, respectively.
389 The former and latter clusters appeared to be associated with N1-P2 complex and P3 components,
390 respectively. There were no significant clusters showing a paragraph-length effect. Topographic maps
391 of the resulting regression coefficients averaged over time periods of either 0.1-0.2 or 0.4-0.5 s from
392 fixation onsets (Figure 2b) showed that the sentence-length effect appeared from the frontal to central
393 regions.

394

395 Figure 2c shows fixation-related time-frequency maps for the raw (ocular-artifact uncorrected) and
396 corrected EEG powers averaged over all electrodes. In the corrected time-frequency map, the power
397 at the fixation onset, which is thought to reflect ocular artifact, was greatly reduced. However, the
398 power in the low frequency band in the period of > 0.8 s, which was influenced by eye blinks at > 1 s,
399 remained uncorrected. In the analysis of fixation-related time-frequency EEG power, there were 344
400 clusters of (electrode, time, frequency)-samples (187 positive and 137 negative) in the sentence-length
401 comparison and 317 clusters of samples (162 positive and 155 negative) in the paragraph-length
402 comparison. Only one positive cluster, for the theta-band in the paragraph-length comparison ($p =$
403 0.038), had a Monte Carlo p -value that was less than 0.025 . There were no significant clusters in the
404 sentence-length comparison. Figure 2d shows the fixation-related time-frequency map for regression
405 coefficients averaged over all electrodes in the paragraph-length comparison. The topographic maps
406 of the resulting regression coefficients of theta-band EEG power averaged over time periods of either
407 0.0 - 0.4 or 0.4 - 0.8 s from fixation onsets (Figure 2e) showed that the paragraph-length effect appeared
408 over the occipital region and left fronto-temporal region.

409

410 No eye movement-related parameters showed a significant correlation to subsequent memory in
411 sentence-length or in paragraph-length comparisons (saccade size; sentence-length correlation, $t(12)$
412 $= 1.15$, $p = 0.27$, paragraph-length correlation, $t(12) = 0.47$, $p = 0.64$, fixation duration; sentence-length
413 correlation, $t(12) = -1.93$, $p = 0.08$; paragraph-length correlation, $t(12) = 1.96$, $p = 0.07$). This result
414 suggests that the significant correlation between fixation-related EEG and subsequent memory did not
415 result from contamination by ocular artifacts. An additional analysis using three regressors (sentence-
416 length and paragraph-length text correlations and fixation duration) yielded results that were almost
417 identical (data not shown).

418

419 fMRI results

420 BOLD activities during text reading were analyzed by the time series of text correlations calculated
421 with sentence-length and paragraph-length text comparisons between the text read and the content
422 report. The results show no regions with a positive correlation between BOLD responses and the text
423 correlation (i.e., no regions in which BOLD activity increased upon reading the texts that were
424 highly correlated with the content reports). In contrast, multiple regions showed significant negative
425 correlation between the BOLD response and the text correlations (i.e., BOLD decreases during
426 reading with high correlations between content reports and text being read) (Figure 3; Table 1). The
427 sentence-length NSME was found in bilateral insula (BA13), right inferior frontal gyrus (BA47) and

428 anterior cingulate gyrus (BA32). The paragraph-length NSME was observed in the left hippocampus/
429 parahippocampal gyrus, the right precuneus/ posterior cingulate gyrus (BA31), and the right
430 intraparietal sulcus (BA7).

431

432 Discussion

433 We found that literature reading produced a positive relationship of fixation-related EEG and negative
434 relationship of BOLD activity to subsequent memory as measured by semantic correlation between
435 the text read and the content reports subsequently written by the participants. The following sections
436 discuss the potential importance of these results for the understanding of neural dynamics of memory
437 encoding during literature reading.

438

439 Positive relationship between fixation-related EEG and subsequent memory

440 In the results, the sentence-length and paragraph-length effects were differently associated with FRPs
441 and fixation-related EEG theta, respectively (Figure 2). First, the sentence-length effects were
442 positively associated with N1-P2 and P3 components (Figure 2a). There are no reports, to our
443 knowledge, on the relationship between FRPs and subsequent memory, although many researchers
444 have reported increased P3 ERP components during successful encoding (Fernandez et al., 1999;
445 Klimesch et al., 2000). The current results agree with these data. On the other hand, the current results
446 of the N1-P2 component does not simply agree with previous results; the current results appeared
447 similar to the reading-related ERP components within 100–200 ms (mainly N1, but also the P2
448 component), which is thought to be associated with lexical word access (Sereno et al., 1998; Sereno
449 and Rayner, 2003). However, topographic maps of these results, including both increases and decreases
450 of the reading-related ERP amplitudes in multiple regions, are not directly associated with the current
451 data, except for the left-hemisphere dominance. In addition to FRP, N1 ERP has been extensively
452 investigated and is thought to be associated with visual discrimination process (see a review by
453 Luck et al. (2000)). This suggests that the current result of decreased N1 amplitude indicates a decrease
454 in the visual discrimination process. In summary, the interpretations of the P3 and N1-P2 components
455 could be combined as follows. The decreased lexical access and/or decreased visual discrimination
456 interpreted by the N1-P2 can be explained by many factors, while factors related to “low mnemonic
457 load”, rather than factors related to resting, would agree with the successful encoding interpreted by
458 the P3. Furthermore, the low mnemonic load was speculated to be associated with “known contents”
459 (or a good correspondence to preexisting knowledge during reading) rather than “poor contents,”
460 because enough semantic contents in the read text were required to detect successful encoding by text

461 correlation in the current study. It should be noted that the current results did not include either N1
462 FRP at the occipital region, which was shown to be associated with reading (Henderson et al., 2013),
463 or N400 ERP (Kutas and Hillyard, 1980; Kutas and Federmeier, 2000) and N400 FRP (Dimigen et al.,
464 2011), which are shown to be associated with text comprehension.

465

466 Second, the paragraph-length effect was associated with increased EEG theta (Figures 2d and 2e).
467 There are a number of reports showing increased EEG theta during successful encoding (Klimesch et
468 al., 1996; Weiss and Rappelsberger, 2000; Sederberg et al., 2003; Summerfield and Mangels, 2005;
469 Osipova et al., 2006). The current results agree with these data, except for the topographic maps of the
470 SME; the current results appeared in fronto-temporal and occipital regions, while previous reports
471 differently appeared in frontal (Summerfield and Mangels, 2005; White et al., 2013), central (Klimesch
472 et al., 2001), or temporal regions (Hanslmayr et al., 2011) (see also a review by Hsieh and Ranganath
473 (2014)). Besides the successful encoding, the current results could be also associated with a more
474 extensive mnemonic processes, such as linguistic comprehension associated with left fronto-temporal
475 theta increases (Hagoort et al., 2004), or a higher load of cognitive control associated with left fronto-
476 temporal theta increases (Sauseng et al., 2010).

477

478 **Negative relationship between BOLD activity and subsequent memory**

479 Increases (Brewer, 1998; Wagner, 1998) as well as decreases (Otten and Rugg, 2001; Wagner and
480 Davachi, 2001; Daselaar et al., 2004; de Chastelaine and Rugg, 2014) in BOLD activity have both
481 been reported during successful encoding (see also the review by Kim (2011)). Our results failed to
482 identify regions showing positive relationships between BOLD signals and subsequent memory, while
483 multiple regions showed negative correlations with subsequent memory (i.e., NSME), with the
484 bilateral insula, right inferior frontal gyrus and anterior cingulate gyrus showing the sentence-length
485 effect and the left hippocampus/ parahippocampal gyrus, the right precuneus/cingulate gyrus, and the
486 right inferior frontal gyrus showing the paragraph-length effect (Figure 3; Table 1).

487

488 For the interpretation of the current results, the overlaps of the resultant regions with SME/NSME
489 regions and other functional networks in previous reports were computed (Table 2). Surprisingly, the
490 current results were found to be not well correlated with the regions showing NSME in a previous
491 report (Kim, 2011), suggesting that the regions showing negative relationships to subsequent memory
492 do not simply reflect successful memory encoding. The regions showing a sentence-length effect are
493 primarily associated with the anterior salience network (Menon and Uddin, 2010), which functions to

494 identify the most relevant among several internal and extra-personal stimuli in order to guide behavior.
495 In contrast, the regions showing a paragraph-length effect largely overlapped with the default mode
496 network (DMN) (Raichle et al., 2001), which is known to be activated during relaxed non-task states
497 and self-oriented cognition, such as mind wandering or autobiographical memory retrieval, and is
498 deactivated during performing cognitive tasks (see reviews (Buckner et al., 2008; Raichle, 2015)).

499

500 The result of sentence-length NSME in the salience network could superficially produce a
501 contradictive interpretation, i.e., successful encoding was associated with decreased attention to the
502 text. However, this can be solved by considering the details of the decreased attention as follows. The
503 salience network was thought to be continuously activated during reading, while its activity is
504 supposed to be relatively decreased during the reading of texts characterized by low mnemonic load,
505 such as “known texts,” as illustrated by the EEG sentence-length effect. Cognitive factors related to
506 resting, e.g., low wakefulness or low interest to the text, were also associated with decreased attention
507 to the text. However, these effects, of which time-course was supposed to be longer than the time-
508 course of individual sentence reading, were expected to be regressed out from the sentence-length
509 effects in the current multiple regressions analysis, and that would be dominant in the paragraph-length
510 effect. The texts characterized by low mnemonic load were supposed to be easily memorized, thus the
511 sentence-length NSME in the salience network is explained

512

513 The result of paragraph-length NSME in the DMN was explained by the suppression of task-irrelevant
514 internal thoughts (Anticevic et al., 2012) and the effective allocation of cortical resources (Hasson et
515 al., 2007). In contrast to the salience network, the DMN was thought to be continuously deactivated
516 during reading, while the DMN could be more strongly deactivated during higher efforts of reading
517 when task-irrelevant internal thoughts were more strongly suppressed. During such periods, the
518 encoding performance was also supposed to be better. As a result, the paragraph-length NSME in the
519 DMN would appear. As discussed above, with the consideration of the time course of the task-
520 irrelevant internal thoughts, this effect would likely appear as a paragraph-length effect, rather than a
521 sentence-length effect.

522

523 The results of NSMEs in both the salience network and the DMN seemingly contradict that these
524 networks are usually known to have opposite activation patterns. However, this is simply solved by
525 considering the differences of the time-courses of the detected BOLD signals in these networks. In the
526 current essays used, the average paragraph-length was two-and-a-half-times longer than the average

527 sentence-length (See EEG Methods/Stimuli); accordingly, the time-course of the paragraph-length
528 regressors was sufficiently longer than the time-course of the sentence-length regressor. Thus, it was
529 thought that the NSMEs in the salience network and the DMN were not contradictory, but instead
530 reflected differences in cognitive aspects in different time-courses; the former reflected the reading of
531 individual sentences characterized by low mnemonic load and the latter reflected the cognitive states
532 related to the suppression of task-irreverent thoughts.

533

534 The hippocampus usually showed a positive SME, but our results showed an NSME for the left
535 hippocampus/parahippocampal gyrus. This failure to detect increased BOLD activity during successful
536 encoding may be explained by the long-lasting reading (~10 min) in the current task, in which the
537 regions associated with subsequent memory were continuously activated. A relatively small fluctuation
538 dependent on subsequent memory may be obscured by a more general pattern of task-related
539 deactivation, as pointed out by Yarkoni et al. (2008). Recently, Baldassano et al. (2017) demonstrated
540 that the hippocampus was specifically activated at the end of an event, while the average hippocampal
541 activity was decreased during the event. This may also explain the current result.

542

543 Relationship between fixation-related EEG and BOLD activity

544 Simultaneous fMRI-EEG measurements have demonstrated an inverse correlation between frontal
545 EEG theta and BOLD activity in the DMN during resting (Scheeringa et al., 2008), mental arithmetic
546 (Mizuhara et al., 2004), and memory encoding (White et al., 2013). The current results for the
547 paragraph-length comparison showed a negative relationship with fronto-temporal EEG theta and a
548 positive relationship with BOLD activity in the DMN, which is in agreement with these previous
549 reports.

550

551 On the other hand, combined ERP-fMRI studies have demonstrated a positive correlation between P3a
552 components (an earlier subcomponent of P3) and BOLD activities in frontal areas and the insula during
553 oddball tasks (Bledowski et al., 2004), and in the anterior cingulate during spatial attention tasks
554 (Bengson et al., 2015). The current results of the sentence-length comparison, showing a positive
555 relationship with N1-P2 and P3 FRP components and a negative relationship with BOLD activity in
556 the salience network, does not agree with these previous reports. This might be explained by
557 differences in the cognitive tasks; the current task of natural reading required more complicated
558 cognitive processes than the tasks described in the previous reports. Another reason is thought that
559 ERPs originating from phase resetting might not induce major changes in local brain metabolism, as

560 pointed out by Debener et al. (2006).

561

562 Text correlation as an index of subsequent memory

563 There are different levels of text comprehension; textbase comprehension is the encoding of the
564 meaning of the text and situation model construction is further supplemented by preexisting knowledge
565 needed for coherent understanding (Kintsch, 1994). Free-recall tasks have been typically used for the
566 evaluation of textbase comprehension; however, the text correlation used in the current study was
567 thought to measure subsequent memory associated with both the textbase and situation model. One
568 reason for this was that the text read was long enough (~ 8 and 4 thousand words, i.e., ~ 30 and 15 min
569 of reading, in EEG and fMRI experiments, respectively) to allow memorization of phrases in the text;
570 however, semantic context and preexisting knowledge were still available during reading as effective
571 guides for encoding. This may lead participants to use a strategy that falls within the situation model
572 for the encoding of text. This was partially supported by the results of content reports, each of which
573 consisted of a small number of words (~10% of the text read), but included abstract representations of
574 the text read. On the other hand, the possible use of preexisting knowledge during reading may produce
575 a problematic variation in encoding strategies. Unfortunately, the current study cannot rule out this
576 possibility; however, behavioral results showing no explicit outliers in reading time and the word
577 number of content reports suggests a relatively small variation in participant encoding strategies.

578

579 In summary, our results demonstrated (1) the availability of semantic correlation of text, based on a
580 recent natural language processing procedure, to detect brain activities related to context-dependent
581 memory; (2) the positive relationship of FRP and fixation-related EEG theta and negative relationship
582 of BOLD activity with subsequent memory; and (3) the different time-courses of memory-related
583 activities in the salience network and the DMN during reading, in which the sentence-length encoding
584 was associated with salience network deactivation (thought to reflect the reading of sentences
585 characterized by low mnemonic load), and the paragraph-length encoding was associated with the
586 DMN deactivation (thought to reflect the suppression of task-irrelevant thoughts during reading). It
587 has been suggested that context-dependent memory encoding during natural reading of literature
588 requires large-scale network deactivation that might reflect the coordination of a range of voluntary
589 processes during reading.

590

591 Figure captions

592 Figure 1

593 Computation of text correlations between the text that was read and the content report subsequently
594 written by the participants. (a) Schematic procedure for text comparison. Each text and content report
595 was translated into a semantic vector consisting of intermediate semantic features computed from
596 word-collocation in a large text database. The correlation of the vectors represents the semantic
597 similarity between the two texts rather than the appearance of specific keywords (see text for details).
598 (b) Performance of EEG and fMRI participants. Blue and red plots indicate the participants in the EEG
599 and fMRI experiments, respectively. Horizontal and vertical axes denote the performance (the entire
600 text correlation between the text read and the content report) and the surrogate text correlation,
601 respectively. The fact that plots lie below the diagonal line shows that the content reports specifically
602 reflected the texts read. The data from two participants, for whom the plots appeared along the diagonal
603 line and whose correlations were below 0.6, were excluded from the analysis.

604

605 Figure 2

606 Results of fixation-related EEG analysis. (a) Fixation-related potentials (FRPs) of grand averaged
607 signal over all electrodes. The upper plot shows the FRPs. The red and blue plots show FRPs during
608 higher and lower text correlation between the read text and content reports, respectively. The “higher”
609 and “lower” regression coefficients were defined by a median split of the regression coefficients. The
610 gray plots show uncorrected FRP. Horizontal bars indicate time points showing significant effects (p
611 < 0.05). Multiple comparisons were corrected by the nonparametric clustering permutation test (Maris
612 and Oostenveld, 2007). The horizontal axis represents the time from fixation onset. The lower plot
613 shows horizontal and vertical EOGs (HEOG and VEOG). (b) Topographical head maps of regression
614 coefficients of the sentence-length text correlation in the time periods 0.1-0.2 s and 0.4-0.5 s. (c) Time-
615 frequency maps of raw (ocular-artifact-uncorrected) and corrected EEG power. The horizontal axis
616 represents the time from fixation onset; vertical axis indicates frequency on a logarithmic scale. (d)
617 Time-frequency map of regression coefficients averaged over all channels for the paragraph-length
618 text correlations between the text read and the content report. The values were masked by a cluster-
619 based statistical value ($p < 0.05$). (e) Topographical head maps of regression coefficients of the
620 sentence-length and paragraph-length text correlations in theta-band (4 - 8 Hz) EEG. The maps of
621 regression coefficients were averaged over the time periods 0 - 0.4 s and 0.4 - 0.8 s.

622

623 Figure 3

624 Brain regions showing a significant decrease in BOLD activity during reading of texts that were highly
625 correlated with the content reports subsequently written by the participants. The results of sentence-
626 length text correlation are shown on the top and in the middle, and those relevant to paragraph-length
627 text correlation are shown on the bottom. There were no significant regions showing positive
628 subsequent memory effect (i.e., BOLD activity increasing during reading of texts that were highly
629 correlated with the content reports).

630

631 Table 1

632 Brain regions showing a significant decrease in BOLD activity correlated with sentence-length and
633 paragraph-length text correlations.

634

635 Table 2

636 Volume overlap ratio of the NSME regions in this study with previously reported functional networks.
637 SME/NSME networks were defined by multiple spheres of which locations and volumes were given
638 by SME (verbal associative subgroup) and NSME (verbal item subgroup) (Table 3 and 6 in Kim (2011),
639 respectively). Functional ROIs reported by Shirer et al. (2012) were analyzed. 6/14 functional
640 networks showing significant overlap are listed in the table. Volume overlap was defined by
641 (overlapped voxels)/(#voxels in the ROI). Each functional network was inflated ± 1 voxel (3 mm) to
642 give stable overlap. * indicates significance at the level of $p < 0.05$ with FDR correction ($q < 0.05$),
643 with a null hypothesis of “volume overlap ratio between ROIs and functional regions is equal to the
644 volume ratio of the region to the domain (voxels included in every network)”. ASN; anterior salience
645 network, dDMN and vDMN; dorsal and ventral default mode networks, PN; precuneus network,
646 LECN; left-executive control network, VSN; visuospatial network.

647

648

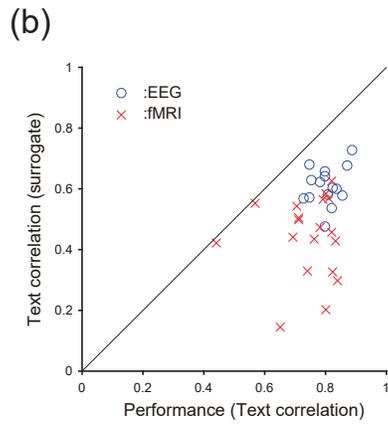
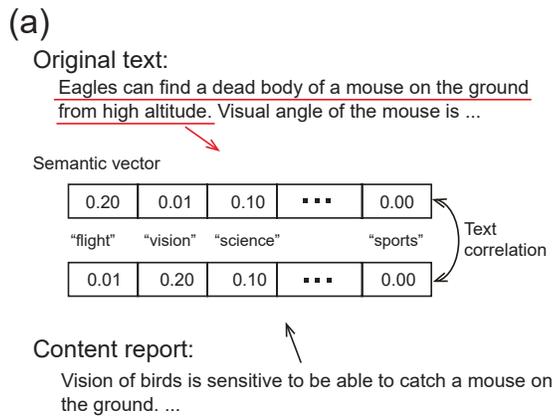
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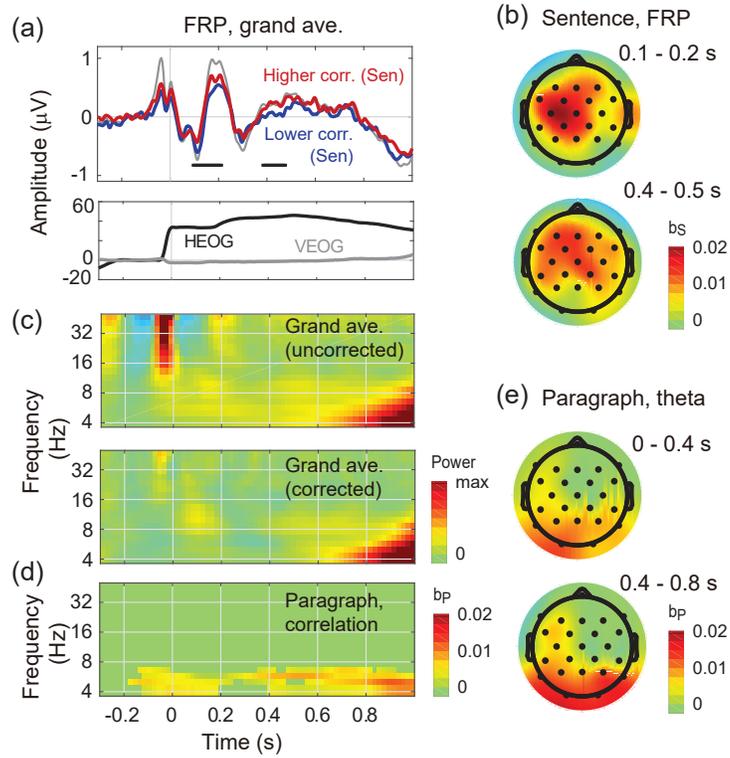
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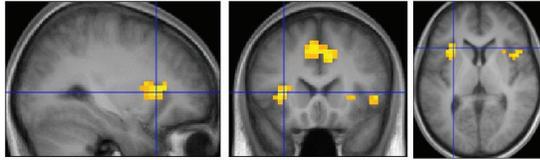
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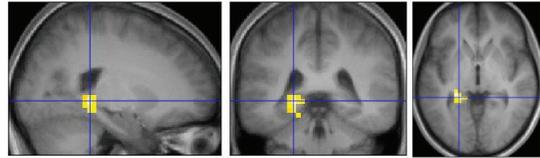




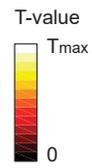
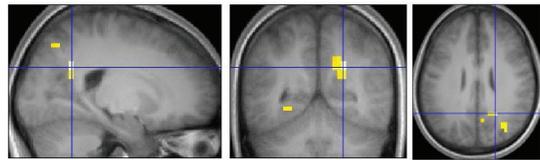
Sentence (-30, 20, 6), T=5.24



Paragraph (-22, -40, -2), T=6.18



Paragraph (22, -56, 30), T=6.03



Anatomical region	MNI coordinates (mm)			t-value
	x	y	z	
Sentence-length (NSME)				
R-Insula (BA13)	50	0	-10	7.09
R-Inferior Frontal Gyrus (BA47)	46	16	2	4.61
R-Cingulate Gyrus (BA32)	10	24	38	5.90
L-Cingulate Gyrus (BA32)	-10	24	42	5.22
L-Insula (BA13)	-30	20	6	5.24
Paragraph-length (NSME)				
L-Hippocampus/Parahippocampal Gyrus (BA36)	-22	-40	-2	6.18
R-Precuneus/Cingulate Gyrus (BA31)	22	-56	30	6.03
R-Intraparietal Sulcus (BA7)	30	-72	38	4.76

p<0.001 (uncorrected) with a cluster-wise FDR of p<0.05

Anatomical region	SME/NSME networks (Kim, 2011)		Functional networks (Shirer et al., 2012)					
	SME	NSME	ASN	dDMN	vDMN	PN	LECN	VSN
Sentence-length NSME								
Cingulate Gyrus			0.92 [*]	0.15			0.03	
L-Insula			0.40 [*]					
R-Insula/Inferior Frontal Gyrus	0.41 [*]		0.37 [*]					0.05
Paragraph-length NSME								
R-Precuneus/Cingulate Gyrus		0.18 [*]	0.41 [*]	0.20	0.37 [*]			0.04
L-Hippocampus/Parahippocampal Gyrus			0.01	0.04				
R-Intraparietal Sulcus				0.35 [*]	0.11	0.51 [*]	0.37 [*]	