The generation effect: Activating broad neural circuits during memory encoding

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Research report

Abstract

The generation effect is a robust memory phenomenon in which actively producing material during encoding acts to improve later memory performance. In a functional magnetic resonance imaging (fMRI) analysis, we explored the neural basis of this effect. During encoding, participants generated synonyms from word-fragment cues (e.g., GARBAGE-W_ST_) or read other synonym pairs (e.g., GARBAGE-WASTE). Compared to simply reading target words, generating target words significantly improved later recognition memory performance. During encoding, this benefit was associated with a broad neural network that involved both prefrontal (inferior frontal gyrus, middle frontal gyrus) and posterior cortex (inferior temporal gyrus, lateral occipital cortex, parahippocampal gyrus, ventral posterior parietal cortex). These findings define the prefrontal-posterior cortical dynamics associated with the mnemonic benefits underlying the generation effect.

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1. Introduction

Psychologists and educators have long extolled the importance of mnemonic techniques for active learning, such as organizing material, monitoring learning, and practicing retrieval (Karpicke and Blunt, 2011; Metcalfe and Kornell, 2007; Roediger and Karpicke, 2006). In one study (Karpicke and Roediger, 2008), individuals learned Swahili–English word pairs (e.g., mashua-boat) and practiced retrieving the English words associated with the Swahili referents (e.g., mashua-?). Compared to simply reading the word pairs, retrieval practice significantly improved memory. Such findings demonstrate the importance of self-generating information—a phenomenon psychologists call the generation effect (Bertsch et al., 2007; Slamecka and Graf, 1978). The benefits of generation have been observed for many kinds of materials, including verbal information (Bertsch et al., 2007; Slamecka and Graf, 1978), arithmetic problems (Smith and Healy, 1998) and pictures (Kinjo and Snodgrass, 2000). It has also been useful as a way of facilitating memory encoding in older adults (Taconnat and Isingrini, 2004; Taconnat et al., 2006) and neurological patients (Lengenfelder et al., 2007; Souliez et al., 1996).

Psychological theories have suggested that the generation effect is driven by a host of internally mediated, top-down processes, such as conceptual analysis (Jacoby, 1983), semantic integration (McElroy, 1987), item distinctiveness...
and selective attention (Jurica and Shimamura, 1999; Tyler et al., 1979). Such processes may be defined more distinctly by addressing the neural processes that drive the generation effect. Yet despite extensive behavioral analyses (for review see, Bertsch et al., 2007), no published study, to our knowledge, has assessed the neural correlates of the generation effect. Candidate structures that could potentially drive this active encoding effect include those involved in top–down executive processing. For example, semantic retrieval and conceptual analysis, which lead to elaborative, long-lasting memory traces (Craik and Lockhart, 1972), have been linked to activity in the left inferior frontal gyrus (IFG) (Bookheimer, 2002; Baker et al., 2001; Poldrack et al., 1999). Other prefrontal regions, particularly in the dorsolateral prefrontal cortex (dPFC), such as the middle frontal gyrus (MFG), have been associated with other executive control processes presumed to interact dynamically with posterior regions (see Miller and Cohen, 2001; Shimamura, 2000, 2008). For example, dPFC regions have been associated with a variety of working memory processes that lead to long-term memory formation (Paller and Wagner, 2002), such as refreshing perceptual features, maintaining items in memory, manipulating information, and selecting items for retrieval (Cohen et al., 1997; D’Esposito et al., 1997, 1999; Johnson et al., 2005; Postle, 2006; Raye et al., 2002; Thompson-Schill et al., 1997).

To the extent that the generation effect is mediated by item distinctiveness, it may be that posterior regions involved in verbal or item analysis, such as the left middle temporal gyrus (MTG) and lateral occipital cortex (LOC) (Binder et al., 2009; Cabeza and Nyberg, 2000; Malach et al., 1995) also become particularly involved. Additionally, one might predict increased activation in the anterior cingulate cortex (ACC), which is involved in conflict monitoring (van Veen et al., 2001) and verbal generation (Barch et al., 2000). Finally, with respect to monitoring internally or cognitively mediated processing, the generation effect may map onto activation related to the so-called default mode network (DMN), initially observed during periods of “rest”, such as between stimulus presentations (Raichle et al., 2001). The DMN is a set of brain regions that include the dorsal medial prefrontal cortex (dMPFC), ventral medial prefrontal cortex (vMPFC), posterior cingulate cortex (PCC), inferior parietal lobule (IPL), precuneus (PrC), retrosplenial cortex (Rsp), lateral temporal cortex (LTC), and hippocampal formation. Upon further analysis, this network has been associated with various internally mediated processes, such as episodic recollection, prospective memory, and perspective taking (see Buckner et al., 2008; Buckner and Carroll, 2007; Spreng et al., 2009). Given the view that the generation effect is involved in internally mediated processing, one might expect greater DMN activation during encoding for generate versus read items.

With respect to long-term memory processes, activity in the IFG during encoding has been particularly associated with successful retrieval (Brewer et al., 1998; Wagner et al., 1998; for review see Paller and Wagner, 2002). Specifically, the IFG is more active during encoding for items subsequently remembered compared to those subsequently forgotten. This effect is robust and has been observed in a variety of tasks and conditions (see Paller and Wagner, 2002). In addition to the IFG, generation may increase activity in other areas also associated with this subsequent memory effect, including the frontal operculum (FOP), fusiform gyrus (FG), inferior temporal gyrus (ITG), cingulate gyrus, dorsal posterior parietal cortex (dPCC), and LOC (see Cansino et al., 2002; Kirchhoff et al., 2000; Uncapher and Wagner, 2009; Wagner et al., 1998).

In the present study, we employed a prototypical memory paradigm used to assess the generation effect. Participants were shown related word pairs in the form of a cue word and word fragment (e.g., QUARREL–F.GHT) and asked to complete the second word in each pair. These encoding trials were compared to trials in which participants simply read related pairs (e.g., QUARREL–FIGHT) (Fig. 1A). At test, old/new recognition memory for the second word in each pair was assessed with confidence ratings (high vs low) (Fig. 1B). Participants were scanned during both study and test phases to identify the neural substrates underlying the generation effect.

2. Materials and methods

2.1. Participants

Twenty-four healthy individuals (13 females, 11 males, mean age = 23 years, range = 18–32 years, all right-handed, native English speakers) participated in the study. Informed consent was obtained according to guidelines approved by the UC Berkeley Office for the Protection of Human Subjects. No participants reported any history of neuropsychiatric disorder or recent use of psychoactive medication. Participants were compensated $12 per hour.

2.2. Stimuli

A total of 200 cue-target synonym word pairs were constructed (e.g., GARBAGE–WASTE). One hundred items were presented at study and again at test, while the other 100 items were used as lures at test. Target words were obtained from the MRC Psycholinguistic Database (Wilson, 1988) and consisted of a mean word length of 5.39 letters (range = 3–8 letters), and a mean frequency of 54.32 (range 1–314) (Francis and Kučera, 1982). During encoding, target words were presented in fragmented form (generate condition; e.g., GARBA–G.E.–W.ST.) or in complete form (read condition; e.g., GARBAGE–WASTE). Fragments were created by removing each vowel (unless it began a word) and replacing it with an underline score. The encoding strategy (read vs generate) and mnemonic status (old vs new) of each word were counterbalanced across participants.

2.3. Behavioral procedure

The study phase was presented in two separate scanning blocks, each consisting of a randomized presentation of 25 generate and 25 read trials. For each study trial, the stimulus (either intact or fragmented pairs) was shown for 3 sec which was followed by a 500 msec blank screen and a jittered fixation cross (4–8 sec). Participants were instructed to make a key-press response when they could identify the second word in each pair (i.e., the target word). This procedure encouraged
comparable processing across study conditions, except that fragmented items had to be generated (Fig. 1A).

Following the study set, a 3-min filled retention interval was presented. During this interval, participants were shown 24 simple math equations (e.g., $3 + 5 = 8$) and determined whether the answer was true or false. Thereafter, old/new recognition memory was assessed using the 50 target items and 50 new items. New items were target words from unused word pairs. For each test trial, a word was presented for 500 msec, followed by a 3 sec blank screen, and a jittered response interval (4–8 sec) (Fig. 1B). Participants determined whether a test word was old or new while indicating their confidence (high or low) for each response during the intertrial interval (ITI). They were instructed to respond old with high confidence (HC) only if they were absolutely certain that the test item was presented during the study phase. Thus, we interpret such HC hits to reflect strong recollective responses.

Upon completion of the first study-test block, the behavioral procedure was repeated with a different set of cue-target pairs.

2.4. fMRI acquisition

A 3T Siemens (Erlangen, Germany) Trio scanner housed at the UC Berkeley Brain Imaging Center was used to acquire T1-weighted anatomical images and T2*-weighted echo-planar images (EPIs) (repetition time (TR) = 2000 msec, echo time (TE) = 22 msec, flip angle = 90°, matrix = 128 × 128, FOV = 220 mm, 1.7 × 1.7 in-plane resolution) with GRAPPA (acceleration factor 3). For functional scans, EPIs consisted of 37 axial slices, 2.5 mm thick, oriented to the anterior–posterior commissure (AC–PC), and were acquired in an interleaved order which resulted in whole brain coverage. A total of 155 volumes (run duration = 310 sec) were collected during each of two encoding runs and 255 volumes (run duration = 510 sec) were collected during each of two retrieval runs. The first five volumes of each run were used for magnetization preparation and were removed from future analyses, resulting in 150 and 250 volumes for each encoding and retrieval session, respectively.

For registration purposes, a high resolution magnetization-prepared rapid-acquisition gradient echo (MPRAGE) volume (TR = 2300 msec, TE = 2.98, matrix = 256 × 256, FOV = 256, sagittal plane, slice thickness = 1 mm, 160 slices) and a gradient-echo multislice (GEMS) volume (TR = 250 msec, TE = 3, matrix = 256 × 256, FOV = 220, 3 mm slice thickness, 28 slices) were collected. Due to movement artifacts, eight of the 96 runs were excluded from data analysis.

2.5. fMRI data analysis

All data processing and analyses were performed using the FMRIB Software Library (FSL) toolbox v4.1.4 (http://www.fmrib.ox.ac.uk/fsl; Smith et al., 2004). During preprocessing, brain extraction tool (BET) was applied to each participant’s data to separate brain tissue from skull and dura using a mask...
3. Results

3.1. Behavioral performance

We confirmed the robust benefit afforded by the generation effect. Specifically, the generate condition produced a hit rate that was 22% greater than that for read items [generate hits = 87%, read hits = 65%, t(23) = 9.97, p < .001, false alarm rate = 21%; see Fig. 1C, Table 1]. The difference between the two conditions was even greater when performance was based only on high-confident hits [generate HC hits = 74%, read HC hits = 42%, t(23) = 11.61, p < .001, HC false alarm rate = 7%; see Fig. 1C, Table 1]. As mentioned above, an HC rating was made when participants were absolutely certain that they had seen a test item during the study phase. Given our findings for HC hits, we can assert that the generation effect is particularly potent in driving strong recollective responses. During encoding, the ability to identity targets was high and not significantly different between generated and read targets [generated targets = 98%, read targets = 99%, t(23) = 1.89, p = .07]. Mean latency to identify a target was longer for generated items than read items [generate = 843 msec, read = 670 msec, t(23) = 6.58, p < .001].

3.2. fMRI data

We first assessed memory-related effects by contrasting activations during encoding for items that were subsequently remembered with those that were subsequently forgotten, collapsed across encoding condition. This contrast revealed significant activation in the left LOC. In a second analysis, we assessed items that elicited HC (i.e., strongly recollected) ratings. This contrast revealed significant activation in the left LOC, IFG, ITG, and right precentral gyrus. Thus, with respect to encoding effects, memory-related activity was particularly observed for items remembered with HC (i.e., strong recollections).

We were particularly interested in determining the neural processes that drive contrasts between generate and read conditions. We thus assessed the contrast of generate hits > read hits, which resulted in significant activation in IFG, MFG, LOC, PrC, ITG, intraparietal sulcus (IPS), and ACC (see Fig. 2A, Table 2). The reverse contrast (read hits > generate hits) resulted in no significant activation differences. We next assessed neural activations associated with the generation effect for HC hits (generate > read, HC hits), which revealed activations in bilateral IFG, MFG, LOC, ITG, IPS, PrC and ACC (see Fig. 2B, regions in red, Table 3). The reverse contrast (read > generate, HC hits) revealed activation in bilateral LOC and PrC, and left angular gyrus (AG) (see Fig. 2B, regions in blue, Table 3).

Activations during retrieval were consistent with previous findings of the successful retrieval effect in which hits are compared with correction rejections (CR) (hits > CRs). In the present study, the successful retrieval effect was associated with increased activation in the left IFG, MFG, superior frontal gyrus (SFG), LTC, LOC, ACC, supramarginal gyrus (SMG), and AG (Fig. 3A). This retrieval-based network was observed when

| Table 1 – Recognition accuracy for generate and read conditions. |
|------------------|------------------|-------------|-------------|
|                  | Hit              | False alarm | HC hit      | HC false alarm |
| Generate         | .87              | .21         | .74         | .07           |
| Read             | .65              | .21         | .42         | .07           |
contrasts were restricted to generated items (hits > CRs, generate items, Fig. 3B) or to read items (hits > CRs, read items, Fig. 3C). Direct comparisons of retrieval-based generated versus read items revealed no reliable differences.

To evaluate neural correlates of the generation effect with respect to behavioral performance, we performed a covariate analysis of recognition performance and regional neural responses associated with the generation effect. We used as our covariate of interest overall memory performance (hit–false alarm) and correlated it with the contrast of generate > read hits during encoding. With this analysis, we addressed the degree to which overall memory performance may be mediated by the magnitude of neural activations associated with the generation effect across individuals. As shown in Fig. 4A, memory performance was significantly correlated with activity in the right parahippocampal gyrus (PHG), temporal fusiform cortex, MTG, AG, LOC, and PrC. Thus, the strength of activation within these regions elicited by self-generation at encoding predicted better memory performance. As the generation effect was particularly potent for HC hits, we performed a second covariate analysis in which the behavioral advantage of generation for HC hits (generate HC hit rate–read HC hit rate) was correlated with its neural counterpart, the contrast of generate HC hits > read HC hits. In this analysis, we found correlated activity in the para-cingulate, frontal pole, left ACC, and right SFG (Fig. 4B), suggesting a medial-frontal network underlying the behavioral benefit of generation for producing strong recollective responses (i.e., HC hits).

### 4. Discussion

The present findings addressed the neural correlates of the generation effect. Active generation was associated with a broad set of regions that included the IFG, MFG, ACC, PrC, IPS, ITG, and LOC. Significant prefrontal activity (IFG and MFG) confirmed the role of executive control processes important for establishing long-term memories. Thus, these findings mesh well with studies that have shown that these regions are particularly involved in stimulus refreshing, updating, and semantic access (D’Esposito et al., 1997; Johnson et al., 2005; Raye et al., 2002; Thompson-Schill et al., 1997). For example, previous studies have shown that these PFC regions are active when participants must refresh or re-activate recently presented words, drawings, or patterns (Johnson et al., 2005; Raye et al., 2002). The generation effect can thus be linked to related acts of refreshing and updating, which also involve internally mediated or generated information.

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**Table 2** — Brain regions active at encoding for subsequently remembered items. Generate hit > read hit; Read hit > generate hit (MNI coordinates).

<table>
<thead>
<tr>
<th>Cluster index</th>
<th>BA</th>
<th>Z</th>
<th>x</th>
<th>y</th>
<th>z</th>
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<tr>
<td>Generate hit &gt; read hit</td>
<td></td>
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<tr>
<td>Anterior cingulate gyrus</td>
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<td>Left IFG</td>
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<td>Left LOC</td>
<td>19</td>
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<td>6.13</td>
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<td>–76</td>
<td>32</td>
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<tr>
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<td>Left occipital pole</td>
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<td>5.56</td>
<td>–32</td>
<td>–90</td>
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<tr>
<td>Right occipital pole</td>
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<td>5.71</td>
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<tr>
<td>Left precentral gyrus</td>
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<td>5.95</td>
<td>–44</td>
<td>4</td>
<td>24</td>
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<tr>
<td>Right precentral gyrus</td>
<td>48</td>
<td>5.17</td>
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<td>–42</td>
<td>44</td>
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<tr>
<td>Right superior parietal lobule</td>
<td>7</td>
<td>4.45</td>
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<td>Read hit &gt; generate hit</td>
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<td>No significant activations</td>
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As suggested by theories of executive control (Miller and Cohen, 2001; Shimamura, 2000, 2008), prefrontal mechanisms act to modulate or control posterior cortical activity thus engaging a broad prefrontal-posterior network involved in selecting, maintaining, and manipulating information in working memory. In the present study, generation was associated with both FPC and posterior activity, particularly in regions involved in image generation (ITG) and object processing (LOC) (see D’Esposito et al., 1997; Malach et al., 1995). Thus, the generation effect offers a useful analysis of the neural dynamics associated with executive or metacognitive monitoring and control (D’Esposito et al., 1999; Miller and Cohen, 2001; Postle, 2006; Shimamura, 2008).

Importantly, covariate analyses showed that memory performance could be predicted by the degree to which neural networks associated with the generation effect were active. Specifically, we found that overall memory performance was correlated with increased generate activity in the PHG, visuospatial imagery. Additionally, participants who benefited the most from generation showed the greatest activation in regions known to be important for memory binding and retrieval, such as the PHG, AG, and PrC (see Davachi, 2006).

Recently, Moss et al. (2011) compared activation when participants reread, paraphrased, or explained biology texts. While self-explaining led to the greatest memory benefit, regional activity in ACC, bilateral superior parietal cortex, and left IFG also increased along with complexity of semantic processing. In the present study, different regions within the DMN were active when reading or generating items during encoding (IPL, PrC, dMPFC for generate > read, HC hits; IPL, PrC for read > generate, HC hits), suggesting that the DMN is responsible for internally driven processing, though different regions may mediate different top–down processes. It is possible that on some trials, active generation oriented participants to internally generated information arising from semantic analysis or conceptual processes, while reading kept participants less on-task and allowed for increased mind wandering. It is acknowledged that the DMN is associated with many internally mediate processes and that there may be regional specificity within the network depending on the particular process being engaged (Buckner and Carroll, 2007; Shimamura, 2011; Vilberg and Rugg, 2008). Interestingly, this pattern of activity was observed for both successfully retrieved generated and read items, and there were no differences during retrieval that differentiated remembered items between the two conditions. Within the confines of the encoding conditions used in the study, our findings suggest that a remembered item (hit or high-confident hit) elicits the same pattern of activation during retrieval regardless of whether it was previously generated or read.

At retrieval, successful recognition (hits > CRs) was associated with activation in lateral and medial PFC, two regions associated with memory recollection (Cabeza, 2008; Shimamura, 2011; Vilberg and Rugg, 2008). Interestingly, this pattern of activity was observed for both successfully retrieved generated and read items, and there were no differences during retrieval that differentiated remembered items between the two conditions. Within the confines of the encoding conditions used in the study, our findings suggest that a remembered item (hit or high-confident hit) elicits the same pattern of activation during retrieval regardless of whether it was previously generated or read.

With respect to mapping psychological theories of the generation effect onto our functional magnetic resonance imaging (fMRI) findings, it is clear that multiple brain regions are responsible for different aspects of the mnemonic benefit associated with the generation effect. Certainly, PFC regions involved with semantic analysis, refreshing, and updating are involved in driving the mnemonic benefit associated with the generation effect. However, a host of posterior regions, such...
as the PHG, temporal fusiform cortex, MTG, AG, and LOC, is also involved. It is possible that active generation increases attention and cognitive effort (prefrontal and posterior cortical activation; Miller and Cohen, 2001; Shimamura, 2000, 2008), conceptual and semantic processing (IFG and MTG; Bookheimer, 2002; Poldrack et al., 1999), and item distinctiveness (LOC and ACC; Malach et al., 1995; van Veen et al., 2001). Perhaps one of the reasons memory researchers have not reached a consensus regarding the underlying mechanism of the generation effect is that active generation engages a large range of cognitive processes. Depending on the task at hand, active generation may promote increases in attention, cognitive effort, item distinctiveness, semantic processing, and conceptual processing. Indeed, our findings affirm the fact that these memory-related influences associated particularly with strong recollective responses are driven by a broad network of both PFC and posterior regions during encoding (see Shimamura, 2010).

Acknowledgments

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REFERENCES


Fig. 3 – Statistical activation maps during retrieval. (A) Overall hits > correct rejections. Regional activations include left IFG, MFG, SFG, ITG, MTG, LOC, ACC, SMG, AG. (B) Generate hits > correct rejections. Regional activations include left LOC, ACC, SMG, AG. (C) Read hits > correct rejections. Regional activations include left IFG, MFG, SFG, ITG, MTG, ACC, SMG, AG, PHG.

Fig. 4 – Covariate analyses. (A) Shown in red are regions related to the generation effect (generate > read, all items) that covaried with overall memory performance (hits-false alarms). Regional activations include PHG, MTG, AG, LOC, temporal fusiform cortex, PrC. (B) Shown in red are regions related to the generation effect (generate > read, HC items) that covaried with the behavioral generation effect (HC hits-false alarms). Regional activations include bilateral paracingulate cortex and frontal pole, left ACC, and right SFG.


