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Research report

The generation effect: Activating broad neural circuits during memory encoding

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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.

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

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(Begg et al., 1989; Kinoshita, 1989; Hunt and McDaniel, 1993), and selective attention (Jurica and Shimamur, 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 (dlPFC), 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, dlPFC 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 (dPPC), 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., GARBAGE–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 keypress response when they could identify the second word in each pair (i.e., the target word). This procedure encouraged

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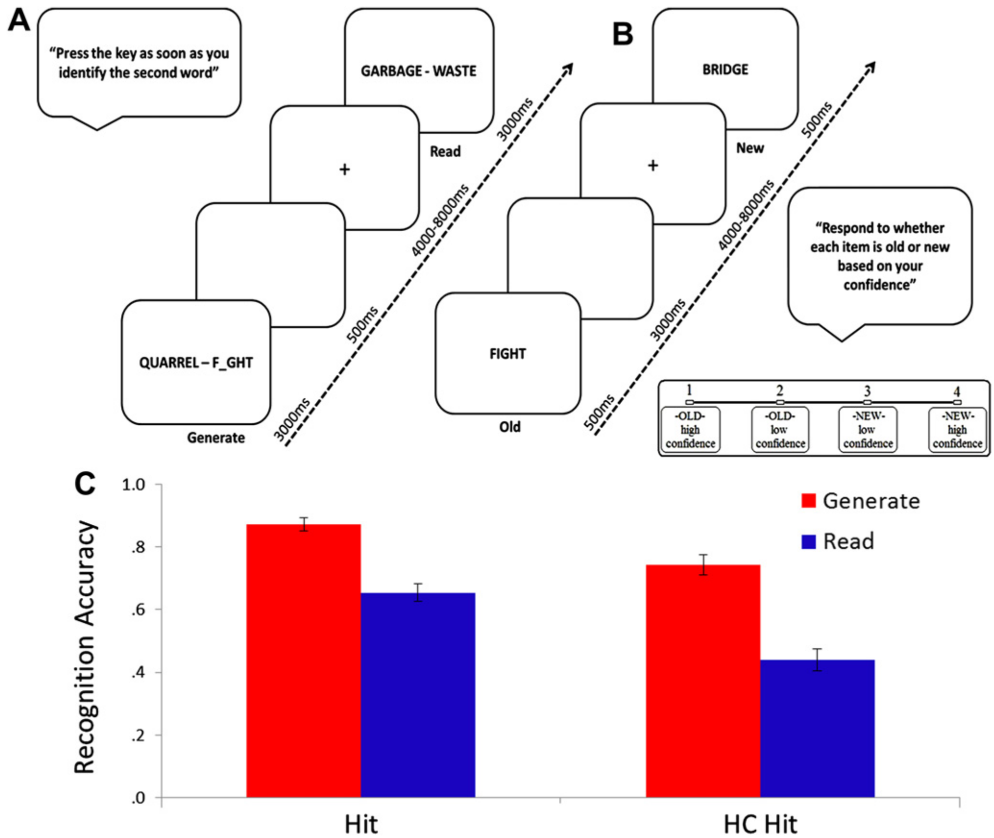

Fig. 1 – Experimental design and behavioral data. (A) Experimental design of encoding phase and (B) retrieval phase. (C) Recognition accuracy for read and generate items. Hits are items correctly identified as old. HC hits are items correctly identified as old with HC.

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

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of the brain from the first volume, which was used for subsequent volumes. Images were then spatially smoothed using a 5 mm full width at half maximum (FWHM) of the Gaussian kernel. To remove low frequency artifacts, highpass temporal filtering was performed with the local Gaussian-weighted fit of a running line. Motion Correction using FMRIB's Linear Image Registration Tool (MCFLIRT) corrected for motion by aligning images to the middle slice with rigid body transformation. Sinc interpolation (Hanning windowed) shifted each slice in the volume in reference to the middle of the TR period. Next, FMRIB's Linear Image Registration Tool (FLIRT) registered subject's EPIs to their skull-stripped high resolution T1-weighted images, which were then registered to standard Montreal Neurological Institute space (FSL's MNI152 template), both of which were combined to transform the EPI's and statistical maps into standard space.

At the first level of analysis, a multilevel, mixed effects general linear model was run using FMRIB's Improved Linear Model (FILM). Each individual run (two encoding and two retrieval runs per participant) was modeled in individual subject space. Next, each resulting statistical map was registered to standard space. Regressors of interest were obtained by convolving stimulus onset times with FSL's canonical (gamma) hemodynamic response function and temporal derivative. Trials in which the participant failed to respond, including those trials in which the participant was unable to identify the target word at encoding, were included in the model as regressors of no interest. Finally, motion parameters were added as a confound variable and temporal autocorrelation was removed through prewhitening.

At the second level of analysis, each subject's two encoding runs were combined, as were each subject's two retrieval runs, using one-sample t-tests. These runs were treated as fixed effects. At the third level, statistical maps were created at the group level for each contrast using FMRIB's Local Analysis of multilevel GLM Mixed Effects (FLAME). The whole-brain family-wise error was corrected to $p < .05$ using Gaussian Random Field theory with a cluster forming threshold of $Z > 2.3$. To assess the relationship between behavioral performance and neural activity, we applied two separate subject-specific covariate analyses. First, we used individual generation effect recollection benefit (generate HC hit rate−read HC hit rate) as a covariate of interest in an analysis of generation effect recollection activity (generate > read, HC hits). We used HC responses to isolate recollection responses and eliminate the confound of varying memory strength and remove possible guess trials. In addition, we used individual memory performance (hit-false alarm score) as a covariate of interest in an analysis of overall generation effect activity (generate > read, all items). Localizations of peak activations were identified by mapping images onto the Harvard-Oxford Cortical Atlas.

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

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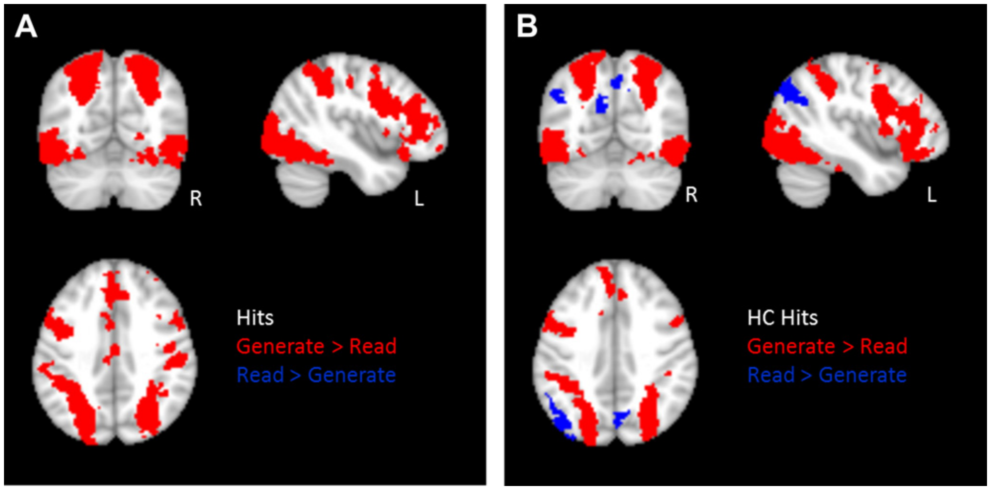

Fig. 2 – Statistical activation maps for the generation effect during encoding. (A) Hits. Generate > read (red): regional activations include bilateral IFG, MFG, LOC, PrC, ITG, IPS, ACC. Read > generate (blue): no significant activation. (B) HC hits. Generate > read (red): regional activations include bilateral IFG, MFG, LOC, ITG, IPS, ACC, right PrC. Read > generate (blue): bilateral LOC, PrC, left AG.

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 paracingulate, 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).

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

Cluster index	BA	Z	x	y	z
Generate hit > read hit					
Anterior cingulate gyrus	24	4.73	0	0	28
Left IFG	48	5.44	−52	14	28
Right IFG	45	4.42	50	34	16
Left ITG	37	4.34	−46	−56	−16
Right ITG	37	4.70	46	−54	−10
Right insular cortex	48	3.10	32	0	10
Left LOC	19	5.98	−24	−76	26
Right LOC	19	6.13	28	−76	32
Left MFG	44	4.78	−54	14	34
Right MFG	45	4.50	52	24	26
Left occipital pole	18	5.56	−32	−90	8
Right occipital pole	18	5.71	34	−92	2
Left precentral gyrus	44	5.95	−44	4	24
Right precentral gyrus	48	5.17	42	8	26
Left PrC	7	3.23	−12	−62	42
Right PrC	7	3.72	18	−58	42
Left superior parietal lobule	40	4.92	−38	−42	44
Right superior parietal lobule	7	4.45	28	−56	48
Read hit > generate hit					
No significant activations					

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.

Table 3 – Brain regions active at encoding for items subsequently remembered with HC. HC generate > HC read; HC read > HC generate (MNI coordinates).

Cluster index	BA	Z	x	y	z
HC generate > HC read					
Left central opercular cortex	48	4.04	−46	6	2
Left cingulate gyrus	32	3.73	−4	40	18
Right cingulate gyrus	24	3.15	4	30	22
Left frontal orbital cortex	47	4.14	−42	26	−6
Left frontal pole	47	3.42	−42	38	−14
Left IFG	45	5.25	−48	34	6
Right IFG	48	3.08	42	16	24
Left ITG	37	3.96	−58	−60	−20
Right ITG	37	5.7	54	−56	−14
Left insular cortex	48	4.38	−32	18	6
Left LOC	19	6.07	−24	−76	28
Right LOC	19	5.58	32	−72	26
Right lingual gyrus	18	3.32	10	−88	−6
Left MFG	45	3.99	−44	30	26
Right MFG	6	3.27	54	10	42
Left occipital FG	19	3.67	−40	−74	−20
Right occipital FG	19	3.47	30	−80	−4
Left occipital pole	18	6.11	−34	−94	10
Right occipital pole	18	5.5	34	−92	2
Left paracingulate gyrus	32	3.35	−4	16	48
Right paracingulate gyrus	32	3.67	12	32	28
Right postcentral gyrus	2	4.54	48	−28	48
Right postcentral gyrus	3	3.22	56	−20	46
Left precentral gyrus	44	6.06	−48	6	26
Right precentral gyrus	44	4.78	44	8	26
Left PrC	18	3.39	−16	−70	−30
Right PrC	19	3.35	24	−64	30
Left SFG	32	3.99	−6	38	42
Left SFG	8	3.6	−4	28	48
Left superior parietal lobule	40	4.95	−36	−48	46
Right superior parietal lobule	7	4.6	32	−54	48
Left SMG	40	4.67	−44	−44	46
Right SMG	2	3.81	44	−36	48
Left temporal occipital fusiform cortex	37	4.39	−44	−56	−16
Right temporal occipital fusiform cortex	37	5.04	44	−58	−12
HC read > HC generate					
Left AG	39	3.37	−48	−68	26
Left LOC	19	3.38	−40	−84	36
Right LOC	7	3.23	8	−68	36
Left occipital pole	19	3.66	−42	−68	36
Left PrC	23	3.43	−10	−68	26
Right PrC	7	3.23	8	−68	36
Right superior parietal lobule	7	3.06	4	−64	48

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 PFC 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, temporal fusiform cortex, MTG, AG, LOC, and PrC. In addition, the behavioral benefit of generating at encoding to produce subsequent HC hits was correlated with activity in medial anterior PFC regions known to be important for attending to internally generated versus externally perceived stimuli (Lagioia et al., 2011; Simons et al., 2006, 2008). These findings link the generation effect to regional activations during encoding that are known to be critical for the establishment of long-term memories (Paller and Wagner, 2002). Generation increased both prefrontal activity and activity in posterior regions involved in verbal processing, object analysis, and 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; Spreng et al., 2009).

At retrieval, successful recognition (hits > CRs) was associated with activation in lateral and medial PPC, 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

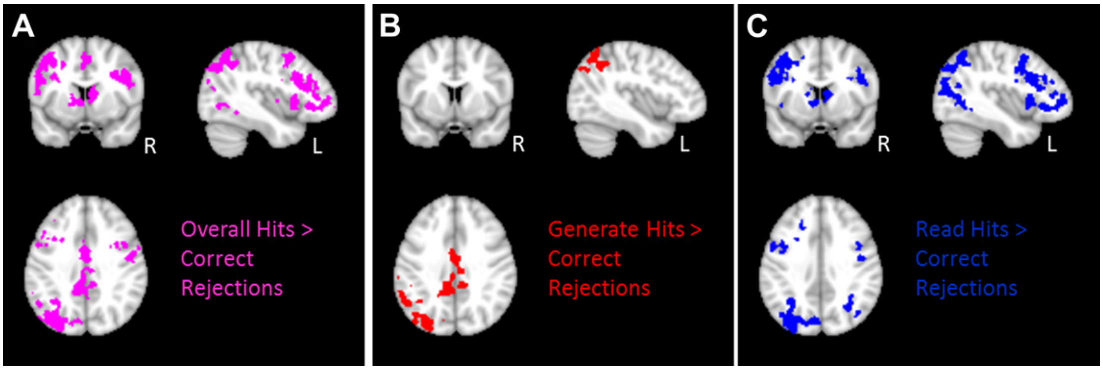

Fig. 3 – Statistical activation maps during retrieval. (A) Overall hits > correct rejections. Regional activations include left IFG, MFG, SFG, ITG, MTG, LOC, ACC, SMG, AG. (B) Generate hits > correct rejections. Regional activations include left LOC, ACC, SMG, AG. (C) Read hits > correct rejections.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

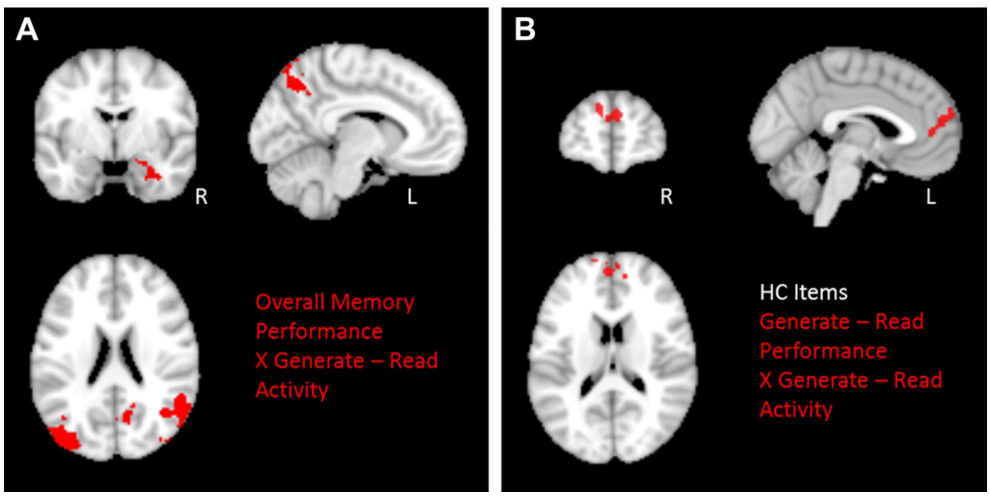

Fig. 4 – Covariate analyses. (A) Shown in red are regions related to the generation effect (generate > read, all items) that covaried with overall memory performance (hits-false alarms). Regional activations include PHG, MTG, AG, LOC, temporal fusiform cortex, PrC. (B) Shown in red are regions related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

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).

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