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Research report

The generation effect: Activating broad neural circuits during memory encoding

Zachary A. Rosner*, Jeremy A. Elman [1] and Arthur P. Shimamura [2]

Department of Psychology, University of California, Berkeley, CA, USA

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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),

* *Corresponding author*. Department of Psychology, Room 3210 Tolman Hall, University of California, Berkeley, CA 94720-1650, USA.
E-mail addresses: zrosner@berkeley.edu (Z.A. Rosner), jelman@berkeley.edu (J.A. Elman), aps@berkeley.edu (A.P. Shimamura).
[1] Tel./fax: +1 510 643 5371.
[2] Tel.: +1 510 642 7131; fax: +1 510 643 5371.

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semantic integration (McElroy, 1987), item distinctiveness (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