

Effects of aging on true and false memory formation: An fMRI study

Nancy A. Dennis^{a,*}, Hongkeun Kim^b, Roberto Cabeza^a

^a Center for Cognitive Neuroscience, Duke University, Durham, NC 27708, United States

^b Department of Rehabilitation Psychology, Daegu University, Daegu 705-714, South Korea

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Abstract

Compared to young, older adults are more likely to forget events that occurred in the past as well as remember events that never happened. Previous studies examining false memories and aging have shown that these memories are more likely to occur when new items share perceptual or semantic similarities with those presented during encoding. It is theorized that decreased item-specific encoding and increased gist encoding contribute to these age differences in memory performance. The current study used a modified version of the Deese–Roediger–McDermott (DRM) paradigm to investigate the neural correlates of true and false memory encoding. Results indicated that, compared to young, older adults showed reduced activity in medial temporal lobes (MTL), left ventrolateral prefrontal cortex (VLPFC), and visual cortices associated with subsequent true memories. Despite these decreases older adults showed increased activity in right VLPFC and left superior temporal gyrus (STG) for subsequent true memories. Age-related increases in STG were also associated with subsequent false memories. Results support the theory that older adults engage in less item-specific encoding and greater gist encoding, and that these increases in gist encoding support both subsequent true and false memories. Furthermore, results extend findings of reduced frontal asymmetry in aging, often found in block designs, to the subsequent memory paradigm. Results suggest that greater bilateral frontal activity during encoding in aging are not just task-related, but may be associated with subsequent successful memory performance.

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1. Introduction

Compared to young adults, older adults are not only more likely to forget events that happened in the past but also to remember events that never happened (Koutstaal & Schacter, 1997; Norman & Schacter, 1997; Tun, Wingfield, Rosen, & Blanchard, 1998). Research has shown that this age-related increase in false memories is especially salient when new items presented during retrieval are closely related to those encountered during encoding (e.g., Kensinger & Schacter, 1999; Koutstaal & Schacter, 1997). For example, in the Deese–Roediger–McDermott (DRM) paradigm, participants who study lists of words that are all semantically related to a

word that is not presented (related lure), show a strong tendency to falsely recall or recognize the related lure at test (Roediger & McDermott, 1995). In this paradigm, older compared to younger adults show both a reduction in accurate retrieval of the words presented in the list and an increase in erroneous retrieval of the related lure (Balota et al., 1999).

Theoretical accounts of the age-related increase in false memories have postulated deficits in memory for item-specific information (Koutstaal & Schacter, 1997; LaVoie & Faulkner, 2000; Norman & Schacter, 1997; Spencer & Raz, 1995; Tun et al., 1998) as well as reliance on semantic gist (Balota et al., 1999; Tun et al., 1998). One theory that incorporates both mechanisms is the fuzzy trace theory. According to this theory, two types of memory traces are created during encoding: item-specific (verbatim) traces and gist traces (Brainerd & Reyna, 1990; Schacter, Verfaellie, & Pradere, 1996). Item-specific traces retain the distinctive features of the individual items, whereas gist traces retain the general meaning of the event, but lack perceptual details or information about specific instances of the encoding

* Corresponding author at: Center for Cognitive Neuroscience, Duke University Box 90999, LSRC Bldg. Durham, NC 27708, United States.

Tel.: +1 919 668 5262; fax: +1 919 681 0815.

E-mail address: ndennis@duke.edu (N.A. Dennis).

event. Both types of memory traces can be employed during retrieval to endorse an item as ‘old’. Fuzzy trace theory can account for age-related increases in false memories by assuming that older adults have a deficit in memory for item-specific traces but not for gist traces (Tun et al., 1998). A positive outcome is that memory for gist traces may partly offset item-specific memory deficits in older adults. In the DRM paradigm, for example, older adults may successfully endorse a studied item as old because it matches the gist trace for the studied list, even if they cannot remember item-specific information for that item. Unfortunately, relying on gist traces in the absence of item-specific traces has the negative side effect of increasing false memories. For instance, in older adults the tendency to endorse the gist-matching related lure is not opposed by item-specific memories indicating that the particular item was not in the study list. The differential effects of aging on memory for item-specific and gist information may occur during encoding and/or during retrieval. In the present study, we used functional neuroimaging to investigate the effects of aging on the neural correlates of encoding gist and item-specific information.

Previous functional neuroimaging studies of encoding and aging have found significant age effects in prefrontal cortex (PFC) and medial temporal lobe (MTL) activity (for a review see Daselaar, Brownlyke, & Cabeza, 2006a). The most typical finding within PFC has been an age-related decrease in left PFC activity coupled with an age-related increase in right PFC activity (e.g., Anderson et al., 2000; Cabeza et al., 1997; Grady et al., 1995). As a result, the pattern of PFC activity tends to be more bilateral in older than in young adults. This finding is consistent with many functional neuroimaging studies that have shown a hemispheric asymmetry reduction in older adults (HAROLD) in other cognitive domains, including episodic retrieval, working memory, attention, and perception (Cabeza, 2002). While the exact role of increased bilaterality in older adults is still under investigation, one theory posits that it may counteract age-related neurocognitive deficits (Cabeza et al., 1997). To investigate this compensation account it is useful to isolate activity associated with successful cognitive processes.

Only a few functional neuroimaging studies of encoding and aging have used a technique that allows for the isolation of brain activity specifically associated with successful encoding processes: the subsequent memory paradigm (see Paller & Wagner, 2002). This method associates successful encoding processes with brain regions that show greater study-phase activity for items that are remembered rather than forgotten in a subsequent memory test. The difference in activity between subsequently remembered versus forgotten items is known as ‘difference in memory’ or Dm (hereafter referred to as true Dm). In young adults, true Dm activity is typically found in ventrolateral PFC and MTL regions (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Davachi, Maril, & Wagner, 2001; Otten & Rugg, 2001; Prince, Daselaar, & Cabeza, 2005; Wagner et al., 1998). To date, only three studies have used the subsequent memory paradigm to investigate the effects of aging on successful encoding activity (Dennis, Daselaar, & Cabeza, 2006; Morcom, Good, Frackowiak, & Rugg, 2003). These studies have yielded two consistent findings. First, compared to young adults, older adults

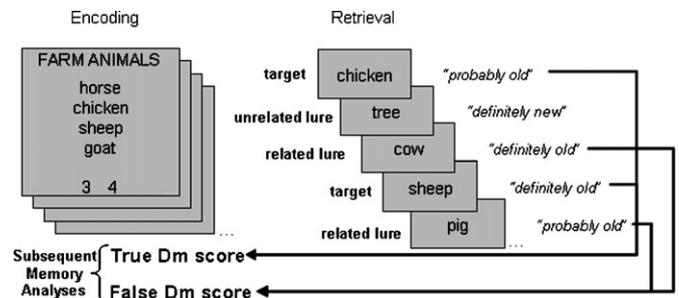


Fig. 1. During encoding participants were presented with short DRM lists. At retrieval they viewed words from the list (targets), new words from different, un-presented categories (unrelated lures), and new words from presented categories (related lures). Participants' memory scores to each word from the list composed the subsequent true recognition (true Dm) score whereas memory scores to the related distractors composed the subsequent false recognition (false Dm) score.

showed reduced true Dm activity in MTL regions (Dennis et al., 2006; Gutchess et al., 2005), possibly reflecting a deficit in the formation of new memory traces. Second, compared to young adults, older adults showed greater true Dm activity in dorso-lateral and anterior PFC regions (Dennis et al., 2006; Gutchess et al., 2005; Morcom et al., 2003), possibly reflecting a compensatory mechanism. In these studies, the finding of bilateral recruitment in older adults (HAROLD) has been less consistent (see however, Morcom et al., 2003), which raises the question of whether this effect can be directly linked to successful encoding operations.

In the present fMRI study we combined the subsequent memory paradigm with a variation of the DRM paradigm in order to investigate the effects of aging on encoding activity leading to subsequent true memories (i.e., true Dm) and on encoding activity leading to subsequent false memories (a ‘false Dm’). As illustrated by Fig. 1, in each encoding trial, participants studied a ‘mini word-list’ comprising four instances (e.g., horse, chicken, sheep, goat) of a semantic category (e.g., farm animal). To promote gist encoding we instructed participants to check if all instances belonged to the category, and included several ‘catch trials’ in which one instance did not match. At test, participants performed an old/new recognition test with confidence ratings that included studied words (e.g., targets: horse, chicken) as well as non-studied words from studied categories (related lures: e.g., cow, pig). Using the subsequent memory procedure we calculated two different measures for each encoding trial: (i) how many (and how confidently) studied words were later remembered (subsequent hit rate); (ii) how many (and how confidently) non-studied semantic associates were later falsely remembered (subsequent false alarm rate). Using these two measures, we conducted parametric analyses of fMRI activity during encoding that identified regions where activity increased as a function of subsequent true memory (true Dm) or as a function of subsequent false memory (false Dm).

Our study had two goals. The first goal was to investigate age-related differences in item-specific encoding in a task that promotes gist processing. In accord with previous subsequent memory studies involving older adults, we predicted that older adults would show age-related decreases in item-specific encoding activity in the MTL coupled with age-related compensatory

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