

Aging and the neural correlates of source memory: over-recruitment and functional reorganization

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Abstract

Behavioral evidence suggests that memory for context (i.e., source memory) is more vulnerable to age-related decline than item memory. It is not clear, however, whether this pattern reflects a specific age-related deficit in context memory or a more general effect of task difficulty. In the present study, we used event-related functional magnetic resonance imaging (fMRI) with healthy younger and older adults to dissociate the effects of age, task (item vs. source memory), and task difficulty (1 vs. 2 study presentations) on patterns of blood oxygen level-dependent (BOLD) signal changes during memory retrieval. Behavioral performance was similar in both age groups, but was sensitive to task and difficulty (item > source; easy > difficult). Data-driven multivariate analyses revealed age differences consistent with age-related overrecruitment of frontoparietal regions during difficult task conditions, and age-related functional reorganization in bilateral frontal and right-lateralized posterior regions that were sensitive to difficulty in younger adults, but to task (i.e., context demand) in older adults. These findings support the hypothesis of a specific context memory deficit in older adults.

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1. Introduction

Recognizing a person to whom you were recently introduced (item recognition) is generally easier than remembering who introduced you to that person (source memory). Both tasks involve episodic long term memory, but the second requires memory for the contextual details of the central event, and is typically associated with worse performance. Normal aging takes a disproportionate toll on context-dependent tasks (e.g., Spaniol et al., 2006). Similar observations were first made nearly 30 years ago (e.g., Burke and Light, 1981) and have since been explained in terms of either general deficits, such as age-related declines in self-initiated processing (e.g., Craik, 1986), frontal lobe

functioning (e.g., Glisky et al., 2001), working memory (e.g., Park and Payer, 2006), perceptual-motor speed (e.g., Siedlecki et al., 2005), and dopaminergic neuromodulation (Li and Sikström, 2002), or in terms of specific deficits, such as age-related declines in recollection (e.g., Jacoby, 1999), memory binding (e.g., Chalfonte and Johnson, 1996), and associative encoding (e.g., Naveh-Benjamin, 2000). In the current study we used functional magnetic resonance imaging (fMRI) to test the hypothesis that aging is associated with specific losses in context processing that can be distinguished from general decrements in response to task difficulty.

Neuroimaging studies have recently started to shed light on the neural underpinnings of age-related changes in context memory, at both encoding and retrieval stages. A recent study (Dennis et al., 2008) examined brain activity linked to successful encoding of item-context associations (face-scene pairings) using event-related fMRI. Successful encoding was measured by the ability to later recognize correct

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face-scene pairings, and brain activity during encoding of remembered stimuli was compared with that for forgotten stimuli. Compared with younger adults, older adults showed reduced recruitment of hippocampal and bilateral dorsolateral prefrontal cortex (PFC) regions during encoding of remembered pairs. This age-related deficit was unique to associative encoding, and was not seen in contrasts capturing successful encoding of item information (faces or scenes; but see Dennis et al., 2007, and Gutchess et al., 2005, for evidence that item encoding may also show underrecruitment of medial temporal areas in older adults). Furthermore, connectivity analyses showed an age-related increase in frontal-hippocampal coupling during associative encoding, along with an age-related decrease in hippocampal connectivity with posterior (e.g., visual processing) regions. The authors interpreted these findings as evidence for an age-related shift toward reliance on frontally mediated control processes during encoding of item-context associations, possibly to compensate for decline in visual processing regions (see also Daselaar et al., 2006; Davis et al., 2008). Age-related reduction in activation of visual regions during successful encoding of visuospatial source information was also reported by Kukolja and colleagues (Kukolja et al., 2009).

Neuroimaging studies of age differences in context memory at the retrieval end have yielded mixed findings. In a working memory version of a source monitoring task, Mitchell and colleagues (2006) observed increased left dorsolateral PFC activation during source memory (format decisions: picture vs. word) compared with item recognition in younger adults, but not in older adults. The authors attributed this finding to an age-related deficit in the monitoring of specific source information during retrieval. Morcom and colleagues (2007), on the other hand, reported age-related activation increases in bilateral anterior PFC and parietal regions during correct conceptual source memory decisions (remembering which of 2 encoding tasks had been performed for a test item). Morcom and colleagues proposed an interpretation of these findings whereby aging is associated with a loss in the efficiency with which brain regions support cognitive performance. In contrast, a third study (Duverne et al., 2008) reported that correct spatial source memory decisions were accompanied by activation in a similar network of regions in younger and older adults when the groups were matched on overall performance, with little evidence for substantial cortical under- or overrecruitment in the older group. Consistent with this finding, Kukolja and colleagues (2009) reported largely similar activation patterns in younger and older adults during successful retrieval of spatial source information. One exception was left anterior hippocampus, where activation was associated with correct spatial source retrieval in younger adults, but with incorrect spatial source retrieval in older adults.

Finally, a more recent study (Rajah et al., 2010) examined spatial and temporal context retrieval for faces in

younger and older adults. Contrasted with item recognition, both types of context retrieval were associated with deactivation in medial anterior PFC and with activation in right dorsolateral PFC in younger adults, but not in older adults. Rajah and colleagues suggested that the first finding may reflect failure on the part of older adults to silence task-irrelevant ruminations, whereas the second may reflect failure to engage in retrieval monitoring that contributes to successful task performance.

Source memory is thought to depend more strongly on recollection than familiarity (e.g., Yonelinas, 2002; but see Mitchell and Johnson, 2009, for a discussion of differences between source-monitoring and dual-process theories). Source memory tasks are sometimes referred to as objective recollection tasks because successful performance probes memory for experimenter-specified (“objective”) contextual details such as the spatial, temporal, or conceptual properties of an event. Two neuroimaging studies have compared younger and older adults in a so-called subjective recollection paradigm, the remember-know procedure (Tulving, 1985). Using this approach in the context of a word recognition task, Daselaar and colleagues (2006) observed reduced recollection-related hippocampal activity in older adults, as well as increased familiarity-related activity in rhinal cortex. Of note, behavioral recollection estimates were lower in older than younger adults in this study, although the 2 age groups were matched on overall old-new recognition performance. Duarte and colleagues (2008) directly compared objective and subjective recollection in younger and older adults, using a picture recognition task that incorporated spatial and temporal source-memory components as well as remember-know ratings. High functioning older adults, who matched the younger adults on item recognition and subjective recollection, demonstrated impaired performance on objective recollection as well as reduced activity in dorsolateral PFC related to objective recollection. Low functioning older adults, whose performance on all behavioral memory indexes was impaired compared with that of younger adults, showed reduced subjective recollection effects in posterior brain regions, in addition to reduced prefrontal activations.

In summary, some neuroimaging studies have shown age-related decrease in the engagement of the hippocampus and of posterior brain regions that support visuospatial processing, during both encoding and retrieval of source information. (Here and throughout this report we use the term “retrieval” loosely, without specific reference to subprocesses which jointly contribute to recognition performance [e.g., cue specification, search, monitoring, and attribution], but which cannot be dissociated with the measures employed in this study.) Additionally, several studies have demonstrated age-related change in anterior, ventrolateral, and dorsolateral PFC activation during retrieval of source information. However, the direction of this change (i.e.,

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