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Age-related differences in the neural correlates mediating false recollection

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ABSTRACT

The current study investigated the effects of aging on the neural basis underlying true and false recollection. Although older adults, compared with younger adults, exhibited equivalent rates of true recollection, age differences in true recollection showed a pattern of activity commonly found among previous memory studies (e.g., age-related decreases in occipital and increases in prefrontal cortices), suggesting reduced retrieval of perceptual details associated with encoding items and a greater reliance on top-down compensatory processing. With regard to false recollection, older adults exhibited significantly greater false recollection yet did not exhibit increased neural processing. They did exhibit decreased activity in prefrontal, parahippocampal gyrus, and occipitoparietal cortex, suggesting a reduced reliance on reconstruction processes mediating false recollection in young. An individual differences analysis in older adults found false recollection rates predicted activity in several regions. including bilateral middle/superior temporal gyrus. Taken together, these results indicate that increases in false recollection in aging may be mediated by reduced access to encoding-related details as well as reliance on semantic gist and familiarity-related neural activity.

1. Introduction

Age-related memory deficits are a prevailing cognitive reality for older adults. Research has found that, compared to young adults, older adults are both more apt to forget details from previous experiences as well as falsely remember erroneous details or memories of past events (Koutstaal and Schacter, 1997; Norman and Schacter, 1997; Tun et al., 1998). Although the majority of neuroimaging research to date has focused on elucidating the neural correlates associated with age-related increases in forgetting, behavioral research has shown that age-related increases in false memories is equally disruptive to memory processing in aging (McCabe et al., 2009). Moreover, a wealth of recent work with regard to dual process theories of memory has shown that these age-related impairments in memory are not ubiquitous but are subject to both how memory is measured (e.g., recall vs. recognition; recollection vs. familiarity) (e.g., Bastin and Van der Linden, 2003; Craik and Mcdowd, 1987; Watson et al., 2004; Yonelinas, 2002) as well as person-to-person variability in behavior (Christensen et al., 1994, 1999; Lindenberger and Baltes, 1997; Nelson and Dannefer, 1992). The current study uses both a Remember/Know/New memory task and individual performance measures to investigate the neural basis of false recollection and interindividual variability associated with age-related increases in false memories.

With regard to dual process theories of memory, age-related memory deficits in retrieval have been linked to significant reductions in true recollection (Bastin and Van der Linden, 2003; Davidson and Glisky, 2002; Parkin and Walter, 1992), whereas familiarity processes appear to remain relatively intact (Bastin and Van der Linden, 2003; Naveh-Benjamin, 2000; Parkin and Walter, 1992). This behavioral dissociation has been found to correspond to a similar dissociation in neural functioning. Specifically, during memory retrieval, brain regions known to mediate recollection (i.e., the hippocampus, early visual cortex, and lateral parietal cortex) (Ally et al., 2008; Daselaar et al., 2006; Duarte et al., 2008; Duverne et al., 2008) show age-related deficits in activation, whereas those that mediate familiarity (i.e., rhinal cortex, occipitoparietal cortex) often show intact or enhanced functioning in aging (Daselaar et al., 2006; Dennis et al., 2008b; Duarte et al., 2010; Dulas and Duarte, 2012; Yonelinas et al., 2007). As such, it is posited that older adults rely to a larger extent on familiarity, as opposed to recollection, when making memory decisions.

The fuzzy trace theory of false memory encapsulates both recollection and familiarity processes in its definition of verbatim and gist traces and, in doing so, provides an appealing framework for understanding age differences in false memories. Specifically, fuzzy trace theory posits that 2 types of memory traces are created during encoding: verbatim traces and gist traces (Brainerd and

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Reyna, 1990). Verbatim traces retain the distinctive features of an event, whereas gist traces retain the general meaning but lack perceptual details or information about specific instances of an encoding event. Thus, encapsulated in the theory are the concepts of recollection (memory for item-specific traces) and familiarity[1] (memory for gist traces). Although accurate memory retrieval can be based on retrieval of either memory trace, false memories typically occur when new items or events elicit retrieval of the gist trace and no verbatim trace is available (or strong enough) to oppose the familiarity elicited by retrieval of the gist trace. In the absence of a verbatim trace of the true event, the gist trace alone may form the basis of a false memory. This of course is especially problematic in aging, in which encoding and retrieval of item-specific information (i.e., verbatim traces) are impaired and gist or familiarity is left relatively intact. Consistent with the fuzzy trace theory, age-related increases in false memories are most pronounced when old and new information share common semantic, perceptual, and/or conceptual characteristics and, as such, share a common gist trace associated with one or more of these properties (Balota et al., 1999; Kensinger and Schacter, 1999; Koutstaal and Schacter, 1997; Norman and Schacter, 1997; Schacter et al., 1997b; Tun et al., 1998). The notion that increased false memories in aging are supported by gist processing at encoding and a reliance on familiarity is consistent with a number of false memory studies (Balota et al., 1999; Benjamin, 2001; Dennis et al., 2007b, 2008b; Duarte et al., 2010; Koutstaal and Schacter, 1997; Koutstaal et al., 1999; Schacter et al., 1999; Tun et al., 1998).

However, not all false memories are reported to be associated with familiarity or gist. Some false memories are associated with high confidence and vivid details, evoking a sense of recollection associated with retrieval of the false memory. Such false memories have been noted to occur across a variety of conditions including when several targets share a similar meaning, such that gist memories for those targets are strong, in the presence of semantically related distracters, and when participants study pictures that converge on a common meaning and the distractor shares this common meaning (Brainerd et al., 2001). In a recent meta-analysis that focused on the separate contributions of recollection and familiarity to age-related memory differences, McCabe et al., 2009 found a medium-to-large effect size with regard to age-related deficits in true recollection ($d = -0.68$) and an equally large effect size associated with age-related increases in false recollection ($d = 0.61$). Although the effect size for age-related increases in false familiarity was also significant ($d = 0.36$), it was substantially smaller than that of false recollection. Hence, results indicate that aging affects both true and false recollection to a similar degree and that the impact of age on false recollection is greater than its impact on familiarity. Given this "recollection mirror effect" (McCabe et al., 2009) and abundant neural evidence showing that recollection and familiarity are mediated by distinct neural substrates that are differentially impaired in aging, this research underscores the need to examine the cognitive and neural basis of age-related increases in false recollection separate from that of false familiarity.

Atlhough examined in behavioral studies, no neuroimaging study has examined the neural correlates of false recollection separate from that of familiarity in older adults. Previous neuroimaging studies either did not use recollection and familiarity judgments at retrieval (Dennis et al., 2008b; Yassa et al., 2011) or had too few false recollection responses to analyze the data (Duarte et al., 2010). Despite these limitations, the previous studies have concluded that age-related reductions in item specific processing in the hippocampus (Dennis et al., 2008b; Duarte et al., 2010; Yassa et al., 2011), combined with gist processing (Dennis et al., 2008b) and reduced differentiation between processing of targets and lures (Duarte et al., 2010; Yassa et al., 2011), contribute to false memories in older adults. However, given that the focus of these studies was not on recollection-related processing, it is difficult to extend these findings to the phenomenon of false recollection.

A recent study from our lab did examine the neural basis for false recollection separate from that of (false) familiarity (Dennis et al., 2012). Results showed that, in young adults, false recollection arose from erroneous reconstruction processes (Dennis et al., 2012). Specifically, both true and false recollection were found to be associated with a largely overlapping retrieval network including activity in bilateral anterior parahippocampal gyrus (PHG), fusiform gyrus, anterior cingulate cortex (ACC), and right superior parietal cortex. We concluded that this activation pattern was consistent with the theory that young adults use the retrieval of details extracted from encoding and engage in memory reconstruction to support both true and false memories. Furthermore, we concluded that although true recollection is based on reconstructing true details from the encoding episode, false recollection represents a faulty form of this reconstruction, also known as content borrowing, whereby recollection of true details are erroneously associated with related lures (Lampinen et al., 2005). This theory accounts not only for activation in recollection-related regions involved in evaluation and monitoring of difficult decisions (i.e., ACC) and confidence judgments (i.e., parietal cortex) but also for the presence of PHG and hippocampus activation (regions involved in the retrieval and reconstruction of episodic details) during false recollection.

However, given observed age deficits in recollection and general reliance on familiarity in aging, we question whether older adults rely on content borrowing and reconstruction during false recollection, especially given that they have difficulty using retrieval of details in support of true recollection. An alternative possibility is that older adults retrieve the gist trace they encoded during study and use this general detail to support recollection of related lures. For example, if studying a group of farm animals or a set of dogs, older adults might recall the semantic label or general gist of the items presented at encoding when viewing new, related items. If this gist trace is strong enough (and is unopposed by a verbatim trace), then it may be enough of an encoding "detail" to support false recollection. In accord with this idea, recent evidence has shown that, whereas an "old" item presented at retrieval serves as a retrieval cue for verbatim traces, a related lure serves as a cue for retrieval of the gist trace (Guerin et al., 2012). Although this gist is generally theorized to support familiarity-based retrieval, the fuzzy trace theory provides an explanation for how it may be used to support false recollection. Specifically, the theory posits that false recollection is based on a strong sense of familiarity, so much so that people misidentify the strong sense of familiarity for recollection (Brainerd et al., 2001). Thus, although participants may report a subjective experience of recollection, the foundation for this response may be based on familiarity elicited by the gist trace and not actual verbatim details.

In addition to considering the distinction between recollection and familiarity with regard to age-related increases in false memories, aging research also highlights the importance of considering person-to-person variability in both cognitive performance and neural activation. A wealth of behavioral research has found aging to be associated with significant increases in inter-individual variability in cognitive performance (e.g., Christensen

[1] We do not imply that the fuzzy trace theory equates gist to familiarity but suggest that the 2 share similar theoretical constructs, and familiarity is more likely to contribute to gist than is recollection (Yonelinas, 2002).