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Review

Age-related differences in medial temporal lobe involvement during conceptual fluency

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ABSTRACT

Not all memory processes are equally affected by aging. A widely accepted hypothesis is that older adults rely more on familiarity-based processing, typically linked with the perirhinal cortex (PRC), in the context of impaired recollection, linked with the hippocampus (HC). However, according to the *dedifferentiation hypothesis*, healthy aging reduces the specialization of MTL memory subregions so that they may mediate different memory processes than in young adults. Using fMRI, we tested this possibility using a conceptual fluency manipulation known to induce familiarity-related PRC activity. The study yielded two main findings. First, although fluency equivalently affected PRC in both young (18–28; N=14) and older (62–80; N=15) adults, it also uniquely affected HC activity in older adults. Second, the fluency manipulation reduced functional connectivity between HC and PRC in young adults, but it increased it in older adults. Taken together, the results suggest that aging may result in reduced specialization of the HC for recollection, such that the HC may be recruited when fluency increases familiarity-based responding.

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1. Introduction

There is wide agreement that subregions of the medial temporal lobe (MTL) make distinct contributions to memory retrieval. Although the processes and representations indexed by MTL regions continue to be debated, a predominant hypothesis is that the hippocampus (HC) contributes more to *recollection*, a rich, context-based form of retrieval, whereas the perirhinal cortex (PRC) contributes more to *familiarity*, a vague sense of memory in the absence of contextual detail (Brown and Aggleton, 2001; Daselaar et al., 2006b; Eichenbaum et al., 2007; Yonelinas et al., 2007). Behavioral studies have shown that older adults rely more on preserved familiarity in contrast to impaired recollection (e.g., Anderson et al., 2008; Bastin and Van der Linden, 2003; Davidson and Glisky, 2002; Jacoby, 1999; Jennings and Jacoby, 1993; Naveh-Benjamin et al., 2009; Spencer and Raz, 1995; Yonelinas, 2002). Consistent with this behavioral data, there is volumetric MRI evidence that age-related atrophy is greater for HC than for PRC (Raz et al., 2005), and fMRI evidence that aging reduces recollection-related HC activity (Dennis et al., 2008; Morcom et al., 2007; but see Persson et al., 2011), but enhances familiarity-related activity in PRC (Daselaar et al., 2006b).

Complicating the interpretation of these fMRI effects, however, is recent evidence of neural reorganization in aging. According to a *dedifferentiation hypothesis*, aging alters the basic organization of cognitive processes in the brain, so that a region that mediates a particular cognitive operation in young adults may mediate different or additional cognitive operations in older adults (for review, see Grady, 2012). This hypothesis has been used to explain findings in the visual recognition domain, where there is evidence that aging alters the organization of object knowledge (faces, houses, chairs, etc.) in ventral occipito-temporal regions (Park et al., 2004). For example, occipito-temporal regions responding to faces and houses tend to be more distinct in young adults and more overlapping in older adults (Park et al., 2012). This latter effect may reflect reduced sensitivity to preferred stimuli (e.g., less activity for faces in face-selective regions) or increased sensitivity to non-preferred stimuli (e.g., greater activity for houses in face-selective regions) (Park et al., 2012).

Recently we found evidence for age-related dedifferentiation in the memory domain. Consistent with the standard distinction between declarative and nondeclarative memory (e.g., Squire et al., 1990), Dennis and Cabeza (2011) found that young adults selectively recruited the MTL for explicit learning and the striatum for implicit learning. In contrast, older adults recruited not only the MTL but also the striatum for explicit learning, and they engaged not only the striatum but also the MTL for implicit learning. Moreover, whereas MTL and striatal activations were negatively correlated in young adults, they were positively correlated in older adults. In other words, these two memory systems seem to be in direct competition in young adults, but are instead co-activated in older adults. Thus, like ventral occipito-temporal cortex, memory systems may be also affected by a process of age-related dedifferentiation.

Although Dennis and Cabeza (2011) found evidence of age-related dedifferentiation between declarative and nondeclarative memory, they did not investigate the possibility of dedifferentiation within different forms of declarative memory, such as recollection vs. familiarity. Interestingly, there is evidence that recollection and familiarity processes become differentiated during childhood development. One study found that in younger children, HC contributes similarly to recollection and familiarity, and only becomes more specialized for recollection as children get older (Ghetti et al., 2010; for review, see Ghetti and Bunge, 2012). Given that dedifferentiation processes during old age are assumed to mirror differentiation processes observed during childhood development, one possible explanation of spared familiarity in older adults is that in old age, familiarity is supported not only by PRC but also by HC.

In the current study, we investigated this hypothesis using a variant of the masked priming paradigm (Jacoby and

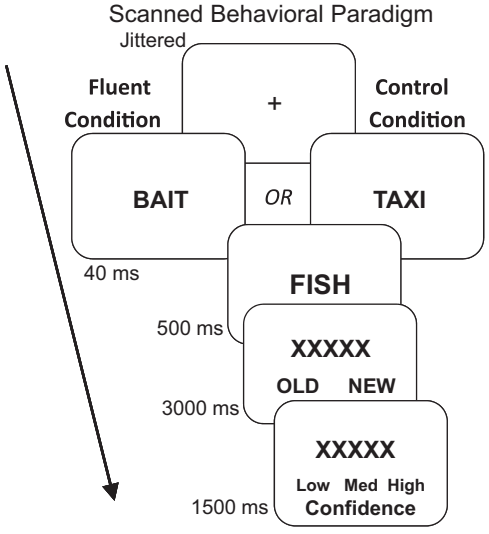

Fig. 1 – Before scanning, participants incidentally encoded a list of words by making semantic judgments (living/nonliving). During scanning, participants viewed old and new words and responded to each one with an old/new decision followed by a confidence rating. The critical manipulation occurred before each recognition item when a 40-ms masked prime was presented. In the *fluent condition*, the masked prime was semantically related to the recognition item (e.g., *bait-fish*), making this item easier to process, whereas in the *control condition*, the masked prime was unrelated to the recognition item (e.g., *taxi-fish*).