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Review

Age-related differences in brain activity in the subsequent memory paradigm: A meta-analysis

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Healthy aging is associated with declines in episodic memory. This reduction is thought to be due in part to age-related differences in encoding-related processes. In the current study, we performed an activation likelihood estimation meta-analysis of functional magnetic resonance imaging (fMRI) studies assessing age-related differences in the neural correlates of episodic encoding. Only studies using the subsequent memory paradigm were included. We found age-related under-recruitment of occipital and fusiform cortex, but over-recruitment in a set of regions including bilateral middle/superior frontal gyri, anterior medial frontal gyrus, precuneus and left inferior parietal lobe. We demonstrate that all of the regions consistently over-recruited by older adults during successful encoding exhibit either direct overlap, or occur in close vicinity to regions consistently involved in unsuccessful encoding in young adults. We discuss the possibility that this overall pattern of age-related differences represents an age-related shift in focus: away from perceptual details, and toward evaluative and personal thoughts and feelings during memory tasks. We discuss whether these age-related differences in brain activation benefit performance in older adults, and additional considerations.

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1. Introduction

Healthy aging is associated with declines in episodic memory (Craik and Salthouse, 2000). Furthermore, memory difficulties represent the most common cognitive complaint in older adults and can diminish their quality of life (Mol et al., 2007). In recent years, many studies have used functional magnetic resonance imaging (fMRI) to examine the neural correlates of episodic memory decline in healthy aging. These studies have typically focused on two stages: encoding and retrieval. In the current study, we focus exclusively on age-related differences in episodic encoding.

Studies assessing age-related differences in fMRI activation have mostly used the subsequent memory paradigm, in which activity related to subsequently remembered events is contrasted against activity related to subsequently forgotten ones. Many of these studies have reported that older adults exhibit reduced activation in various brain regions during successful encoding compared to young adults (age-related under-recruitment). For example, in a study of age-related differences in encoding of pictures of outdoor scenes, Gutchess et al. (2005) reported under-recruitment of bilateral lateral occipital cortex and bilateral parahippocampal gyrus in older vs. younger adults. Age-related decreases in activity are often observed when older adults perform significantly worse than young adults on memory tasks and is thus thought to reflect reductions in older adults' ability in utilizing some cognitive process to the same extent as young adults.

An equally consistent finding in prior fMRI studies of episodic memory is that older adults activate some brain regions to a greater degree than young adults during encoding (age-related over-recruitment). For example, in addition to reporting age-related under-recruitment in occipital and medial temporal lobes, Gutchess et al. (2005) also reported greater activity in bilateral middle/superior frontal gyri (MFG/SFG) and anterior medial FG in older vs. younger adults. In contrast with under-recruitment, there is no straightforward explanation for why older adults would over-recruit some brain regions to perform a task that they do not perform as well as young adults. In their paper, Gutchess et al. (2005) suggested that at least some of the age-related over-recruitment in prefrontal cortex (PFC) may reflect attempted compensation for reduced activation in parahippocampal gyrus.

A variety of theoretical models have been put forward to explain age-related over-recruitment (Cabeza, 2002; Davis et al., 2008; Dennis and Cabeza, 2012; Greenwood, 2007; Maillet and Rajah, 2013b; Park and Reuter-Lorenz, 2009; Rajah and D'Esposito, 2005; Reuter-Lorenz and Cappell, 2008). In general, these models are not specific to episodic memory encoding, but rather attempt to explain this phenomenon across a range of distinct cognitive tasks. In addition, the majority of these models have focused on the PFC as the primary site of age-related over-recruitment, and have suggested that over-recruitment may reflect attempted compensation for declines in other brain regions in the aging brain. For example, the posterior–anterior shift in aging (PASA) model suggests that across different cognitive tasks, PFC over-recruitment may compensate for declines in posterior brain regions, such as occipital cortex (Davis et al., 2008; Dennis and Cabeza, 2008), a proposal similar to the one by Gutchess et al. (2005) in their study of episodic encoding. Another model, the scaffolding theory of aging and cognition, suggests that over-recruitment in older adults represent neural scaffolds, "additional circuitry that shores up declining structures whose functioning has become noisy, inefficient, or both" (p. 183; Park and Reuter-Lorenz, 2009). The PFC is thought to be the primary site of scaffolds, due its versatile and flexible nature. Specifically, the PFC is thought to compensate for declines in functioning in the hippocampus, visual processing regions and the default-mode network (Park and Reuter-Lorenz, 2009).

Although these models provide a useful starting point to understanding age-related over-recruitment, a number of outstanding questions remain within the domain of episodic encoding. First, it remains unclear if specific sub-regions of PFC are consistently over-activated by older adults, or if this over-recruitment is observed throughout the PFC. Some studies suggest that age-related over-recruitment is observed in a specific subset of PFC regions. For example, Gutchess et al. (2005) reported age-equivalent activation in IFG; and over-recruitment in bilateral MFG/SFG and medial FG. Morcom et al. (2003) reported age-equivalent activation in left IFG and MFG, but age-related over-recruitment in bilateral anterior SFG. These findings indicate that only a subset of PFC regions may be over-activated by older adults; yet theoretical models of age-related over-recruitment generally do not make predictions regarding specific regions of PFC. Second, although the PFC has been the main focus of theories of age-related over-recruitment and of individual studies of episodic memory encoding, it remains unclear if PFC is the only region in which older adults consistently exhibit over-recruitment. For example, in Morcom et al. (2003), older adults over-recruited not only bilateral anterior SFG, but also left inferior parietal lobe and medial occipital cortex. In Gutchess et al. (2005), in addition to bilateral MFG/SFG and medial FG, older adults also over-recruited bilateral inferior parietal lobes.

Identifying which brain regions, both in PFC and outside PFC are consistently over-recruited by older adults may be important for understanding which specific component cognitive processes older adults may be utilizing to a greater degree than young adults during episodic encoding. In young adults, different brain regions are thought to be involved in different component processes during episodic encoding. For example, in a recent meta-analysis of studies using the subsequent memory paradigm in young adults, it was reported that bilateral IFG/MFG, bilateral medial temporal lobes (MTL), bilateral occipital/fusiform gyri and bilateral superior parietal cortex are involved in successful encoding (Kim, 2011b). The left IFG was primarily engaged in studies using verbal materials, prompting the author to suggest this region may be involved in controlled semantic/phonological analysis. A posterior region of the IFG was recruited to a greater extent when encoding was associative (e.g., item–context or item–item associations), prompting the author to suggest that this region may be involved in organizational processes. On the other hand, a distinct set of regions including the medial FG, bilateral SFG, posterior cingulate/precuneus, inferior parietal lobes and lingual gyrus were recruited to a greater extent in subsequently forgotten vs. remembered events. The author suggested that these regions might be involved in internally directed attention detrimental to encoding processes. Consistent with this proposal, we found in a recent study that some of these regions including MFG/SFG, posterior cingulate and lingual gyrus were activated during encoding events directly preceding reports of task-unrelated thoughts (TUT) such as mind-wandering in young adults (Maillet and Rajah, 2014). Therefore, assuming that distinct brain regions are involved in specific component processes during episodic encoding in young adults, and assuming relative preservation of the relationship between a brain region and its role in cognition with aging, identifying precisely which brain regions are consistently over-recruited by older adults may yield insight into which cognitive processes are up-regulated in older age.

In the current study, we performed a quantitative activation likelihood estimation (ALE) meta-analysis of age-related differences in brain activation to identify consistent differences in brain activation during successful encoding. One previous quantitative meta-analysis of age-related differences in brain activation at encoding was conducted by Spreng et al. (2010b). In this meta-analysis, it was reported that older adults under-recruited left posterior MFG, putamen, and right medial temporal lobe (MTL), but over-recruited right postcentral gyrus compared to young adults.

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