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Maintenance of youth-like processing protects against false memory in later adulthood

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A R T I C L E I N F O

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ABSTRACT

Normal cognitive aging compromises the ability to form and retrieve associations among features of a memory episode. One indicator of this age-related deficit is older adults' difficulty in detecting and correctly rejecting new associations of familiar items. Comparing 28 younger and 30 older adults on a continuous recognition task with word pairs, we found that older adults whose activation patterns deviate less from the average pattern of younger adults while detecting repaired associations show the following: (1) higher overall memory and fewer false recognitions; (2) stronger functional connectivity of prefrontal regions with middle temporal and parahippocampal gyrus; and (3) higher recall and strategic categorical clustering in an independently assessed free recall task. Deviations from the average young-adult network reflected underactivation of frontoparietal regions instead of overactivation of regions not activated by younger adults. We conclude that maintenance of youth-like task-relevant activation patterns is critical for preserving memory functions in later adulthood.

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1. Introduction

Normal cognitive aging is associated with a decline in the ability to form and retrieve associations among different features of an episode (Old and Naveh-Benimain, 2008; Shing et al., 2010). This general trend of declining associative memory is accompanied by massive individual differences in rates of decline (Ghisletta et al., 2012; Lindenberger and Ghisletta, 2009; Persson et al., 2012). As a result, associative memory is preserved in some older individuals, but not in others (Fandakova et al., 2012). Little is known about the mechanisms driving this heterogeneity (Barulli and Stern, 2013; Nyberg et al., 2012). The general goal of this study is to examine the degree to which individual differences in neural activation and connectivity are related to individual differences in associative memory and false remembering in later adulthood.

Evidence is accumulating that age-related memory deficits are especially pronounced when individuals are required to remember specific contextual details instead of isolated items (Naveh-Benjamin, 2000; Spencer and Raz, 1995). For example, when investigating memory for word pairs in 278 adults (18-85 years), Bender et al. (2010) found that older participants were not only less likely to correctly endorse studied word pairs but were also more likely to falsely endorse repaired associations in which the original words were studied in different configurations (see also Shing et al., 2008). In fact, a direct comparison of the two effects revealed a stronger association between age and false endorsement of repaired associations than between age and failure to recognize intact associations. At the same time, this study revealed a considerable amount of variability among individuals of the same age. For example, in the group of 60- to 80-year-olds, some individuals were almost perfect in correctly detecting repaired associations whereas others wrongly endorsed repaired associations in more than 70% of the cases (see Fig. 1, Bender et al., 2010). This observation is in line with longitudinal observations, indicating increasing heterogeneity of cognitive functions with advancing adult age (de Frias et al., 2007; Ghisletta et al., 2012; Lindenberger and Ghisletta, 2009). Given the notable difficulties of older adults to detect repaired associations of familiar features, the specific goal of this study was to characterize the neural mechanisms underlying heterogeneity in older adults' tendency to falsely recognize associations they have not encountered before. This topic is of great importance for everyday life because it may result in greater susceptibility to misinformation (Jacoby and Rhodes, 2006).

Compared with the detection of novel or intact associations, repaired associations are expected to engage mnemonic control to a greater degree, as single items are highly familiar and need to be





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Fig. 1. Mean activation map of younger adults used to derive functional activation deviation scores for older adults (first row, p < 0.001, uncorrected). Brain regions showing stronger functional activation for correct rejection of rearranged word pairs in high-match compared with low-match older adults (second row, p < 0.05, corrected). There were no regions in which low-match older adults showed stronger activation (p < 0.05, corrected). Coordinates (x, y, z) in MNI standard space.

closely monitored to avoid memory errors (Mitchell and Johnson, 2009). Accordingly, correct rejection of repaired associations typically engages lateral prefrontal cortex (PFC; Lepage et al., 2003), which is known to support mnemonic control over memory contents (Simons and Spiers, 2003).

PFC undergoes declines in both gray and white matter volume in later adulthood (Raz et al., 2005). Compared with younger adults, older adults have shown lower PFC activation during encoding or retrieval of past episodes (Wang et al., 2009). However, other studies have demonstrated additional PFC activation in older adults for memory tasks (Cabeza and Dennis, 2013). In addition, a number of studies have suggested that later adulthood is associated with different patterns of task-related functional connectivity of PFC regions (Daselaar et al., 2006) that are related to individual differences in cognitive performance (Nagel et al., 2011). There is some debate about whether these functional differences reflect corollaries of brain aging (Nyberg et al., 2012), compensatory reactions to age-related declines in posterior brain regions (Cabeza and Dennis, 2013), or the engagement of more neural resources at lower difficulty levels in older adults (Reuter-Lorenz and Cappell, 2008). In any case, the claim that between-person differences in PFC volume, functional activation, and connectivity among older individuals increase from early to later adulthood appears to be well founded (Lindenberger et al., 2013). Thus, the increased heterogeneity in functional activation and connectivity of these regions may contribute to individual differences in associative memory in later adulthood.

The few neuroimaging studies that have examined age differences in encoding or retrieval of associative information provide initial support for PFC contributions to age differences in associative memory (Dennis et al., 2008a; Fandakova et al., 2014; Ford et al., 2010; Giovanello and Schacter, 2012). However, individual differences in neural activation or behavioral performance have not been addressed in these studies. Here, we go beyond mean age differences in neural mechanisms of associative recognition by directly relating differences in neural activation to the observed heterogeneity in associative memory among older adults. We focus our analyses on the correct rejection of repaired associations, a process that requires increased mnemonic control (Mitchell and Johnson, 2009) and poses a substantial challenge to older adults (Jacoby and Rhodes, 2006). Thus, the goals of the present study were to examine the following: (1) the extent to which individual differences in functional activation among older adults, defined as a relative match to functional activations, are related to differences in memory performance; (2) differences between high- and low-match older adults in task-related functional connectivity that may reflect interindividual differences in strategic control of mnemonic content; and (3) whether between-person differences observed on the target memory task generalize to other tasks that presumably require similar mnemonic processes.

To address these issues we scanned younger and older adults working on a continuous recognition task. The task consisted of 3 runs. Within each run, the same set of word pairs was presented once or twice, along with novel and repaired word pairs (for details, see Fandakova et al., 2014). Participants' task was to detect word pair repetitions within the current run while rejecting pairs that were either appearing for the first time within the run, novel, or repaired. Repaired associations were composed by rearranging pairs that had been presented in every run. We hypothesized that correctly rejecting such associations would become easier across runs. This manipulation enabled us to investigate how changing task demands modulated processes involved in associative recognition. Using this paradigm, we previously reported robust mean age differences in a frontal-parietal network involved in the correct rejection of repaired associations (Fandakova et al., 2014). The goal of the present analysis was to delineate the mechanisms underlying individual differences among older adults. Following a method introduced by Düzel et al. (2011), we characterized each older individual's activation pattern in terms of the degree to which it matched the average functional activation pattern of younger adults. Based on recent findings that older adults who showed less functional deviation from younger adults in encoding-related brain activity also showed higher recollection (Düzel et al., 2011), we expected that preserved ability to detect repaired associations of familiar words would be associated with the preservation of

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