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The neural correlates of recollection and retrieval monitoring: Relationships with age and recollection performance

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ABSTRACT

The relationships between age, retrieval-related neural activity, and episodic memory performance were investigated in samples of young (18–29 yrs), middle-aged (43–55 yrs) and older (63–76 yrs) healthy adults. Participants underwent fMRI scanning during an associative recognition test that followed a study task performed on visually presented word pairs. Test items comprised pairs of intact (studied pairs), rearranged (items studied on different trials) and new words. fMRI recollection effects were operationalized as greater activity for studied pairs correctly endorsed as intact than for pairs incorrectly endorsed as rearranged. The reverse contrast was employed to identify retrieval monitoring effects. Robust recollection effects were identified in the core recollection network, comprising the hippocampus, along with parahippocampal and posterior cingulate cortex, left angular gyrus and medial prefrontal cortex. Retrieval monitoring effects were identified in the anterior cingulate and right dorsolateral prefrontal cortex. Neither recollection effects within the core network, nor the monitoring effects differed significantly across the age groups after controlling for individual differences in associative recognition performance. Whole brain analyses did however identify three clusters outside of these regions where recollection effects were greater in the young than in the other age groups. Across-participant regression analyses indicated that the magnitude of hippocampal and medial prefrontal cortex recollection effects, and both of the prefrontal monitoring effects, correlated significantly with memory performance. None of these correlations were moderated by age. The findings suggest that the relationships between memory performance and functional activity in regions consistently implicated in successful recollection and retrieval monitoring are stable across much of the healthy adult lifespan.

Introduction

Episodic memory declines over the adult lifespan, even in individuals seemingly free from age-related neurodegenerative disease (Nilsson, 2003; Rönnlund et al., 2005; Old and Naveh-Benjamin, 2008; Koen and Yonelinas, 2014). This observation has motivated numerous studies in which functional neuroimaging was employed to examine the effects of age on the neural correlates of episodic memory (Grady, 2012). As part of this effort, event-related fMRI has frequently been employed to contrast neural activity in healthy young and older adults during either the successful encoding or, the focus of the present paper, the successful *retrieval* of episodic memories (for reviews see Maillet and Rajah, 2014; Wang and Cabeza, in press).

fMRI studies examining the effects of age on 'retrieval success effects' have typically contrasted the neural activity elicited by test items according to the items' study status and the accuracy of the associated memory judgment. In some of these studies (e.g., Morcom et al., 2007; Duverne et al., 2008; Oedekoven et al., 2015; Angel et al., 2016) the fMRI contrast employed to identify retrieval-related neural activity likely confounded recollection of qualitative information about the study episode with a non-episodic sense of familiarity (Yonelinas, 2002). Recollection and familiarity have distinct neural signatures (Kim, 2010; Johnson et al., 2013) and demonstrate different patterns of age-related decline (Koen and Yonelinas, 2014). Therefore age-related differences in fMRI retrieval-success effects in such studies might reflect the differential mixing of neural activity associated with recollection- and familiarity-based memory judgments, rather than differences specifically in the neural activity supporting recollection of episodic information (Rugg and Morcom, 2005).

Even among studies where this confound is arguably largely absent – for example, where the critical contrast is between correctly recognized test items accorded accurate vs. inaccurate source memory judgments, or items endorsed as 'remembered' vs. 'known' – the findings are inconsistent, ranging from reports of reductions in retrieval-success effects in older compared with younger individuals, to null findings, through to enhanced effects in older participants (e.g., Duarte et al., 2008; Kukolja et al., 2009; Tsukiura et al., 2010; Dulas and Duarte, 2012; Angel et al., 2013; Cansino et al., 2015; Wang et al., 2016; see Wang and Cabeza, in press, for a review).

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Here, we employed fMRI to examine the effects of age on the neural correlates of successful episodic retrieval in a study that, by virtue of the sample size, was substantially more highly powered than its predecessors, and using a memory test widely considered to be heavily dependent on recollection of episodic information. Importantly, although age is a significant source of variance in episodic memory performance, there is substantial variability in performance within groups of similarly aged individuals, and substantial overlap in performance between differently-aged individuals (Nyberg et al., 2012). We took advantage of this variability to assess whether age effects on the neural correlates of episodic retrieval can be identified after variance due to individual differences in memory performance is partialled out. The logic of this approach (see also Oedekoven et al., 2015) is similar to that employed in prior studies where performance on a memory test was equated between older and young samples either by experimental manipulation (Morcom et al., 2007; Duverne et al., 2008; Wang et al., 2009; Angel et al., 2016), or by stratifying participants into high- and low-performing sub-groups (e.g., Duarte et al., 2008). If age effects are evident when performance is equated or controlled for, this would suggest that the neural correlates of retrieval-related activity in older individuals differ from those in young adults, potentially providing insight into the causes and moderators of age-related memory decline (Rugg, in press). By contrast, the absence of age effects when performance is experimentally or statistically equated suggests that the patterns of neural activity associated with successful retrieval in older individuals do not differ from those in young individuals performing at the same level. Such a null finding does not, of course, license the conclusion that a given neural region supporting memory retrieval is *unaffected* by increasing age. Rather, it suggests that increasing age does not modify the relationship between the level of neural activity in the region and memory performance. We return to this issue in the Discussion.

Relatedly, we also examined whether relationships between individual differences in retrieval-related neural activity and memory performance differed across age groups. It has been proposed (e.g., Cabeza et al., 2002; Reuter-Lorenz and Park, 2014), for example, that performance in older adults benefits from age-related neural reorganization (neural 'compensation' or 'scaffolding'). In addition, it is possible that with increasing age performance becomes increasingly sensitive to individual differences in the functional integrity of regions vulnerable to aging (de Chastelaine et al., 2011, 2016). In either case, one might anticipate identifying relationships between neural activity and memory performance that are unique to, or stronger, in older than in young individuals. We have recently reported such findings from the encoding phase of the present study (de Chastelaine et al., 2015, 2016). To anticipate the present results, in contrast to those findings, here we find no evidence that relationships between individual differences in retrieval-related activity and memory performance are modified by age.

In the present study, we contrasted neural activity elicited during successful and unsuccessful retrieval of associative information. We elected to investigate associative memory because it is strongly dependent on episodic recollection (e.g., Mickes et al., 2010) and thus is a relatively 'process-pure' memory test. In addition, associative memory is highly sensitive to age (Old and Naveh-Benjamin, 2008), and the neural correlates of the *encoding* of associative information are already known to differ according to age (de Chastelaine et al., 2011, 2015, 2016; Miller et al., 2008). Three prior fMRI studies examining the effects of age on the neural correlates of episodic retrieval also employed an associative memory procedure (Oedekoven et al., 2013; Dulas and Duarte, 2016; Wang and Giovanello, in press). In the study of Oedekoven et al. (2013), the contrast did not allow for an examination of retrieval success effects but, rather, assessed the activity elicited by test items against baseline. In the studies of Dulas and Duarte (2016) and Wang and Giovanello (in press) where, like here, neural activity for successful versus unsuccessful retrieval of associative memories was contrasted, age-invariant retrieval effects were identified in the hippocampus. In Wang and Giovanello (in press) these effects were accompanied by an additional effect in older particpants in a small region of the left posterior hippocampus. In Dulas and Duarte (2016), enhanced retrieval-related activity was evident in younger participants in several prefrontal regions, but no age effects were reported in cortical regions belonging to the core recollection network (see below).

The present study extends prior research in a second important way. In addition to samples of young and older individuals, we also employed a sample of middle-aged individuals. This age-range has been almost completely neglected in studies examining the neural correlates of episodic memory retrieval (we are aware of only one prior report (Cansino et al., 2015) in which an event-related design was employed to identifiy retrieval-related activity in middle-aged participants (although see Grady et al., 2006, and Kwon et al., in press, for reports of blocked-design studies that included a middle-aged sample)). The inclusion of a group of middle-aged individuals allows for a more continuous sampling of retrieval effects across the lifespan, and hence a more precise assessment of the profiles of any age-related differences in the effects.

A major focus of the present study was a priori analyses directed at two different components of retrieval processing. The first component comprises processes reflected in greater neural activity elicited by retrieval cues associated with successful rather than unsuccessful recollection (operationalized here as associative hits and misses). Recollection-related enhancement of activity ('recollection effects') is consistently observed in what has been termed the 'core recollection network', which comprises the hippocampus, parahippocampal cortex, medial prefrontal cortex (mPFC), left angular gyrus, posterior cingulate, and left middle temporal gyrus (Kim, 2010; Rugg and Vilberg, 2013; King et al., 2015). This network – which overlaps substantially with the well-studied 'default-mode network' (Buckner et al., 2008) – is held to play a key role in initiating successful retrieval, and in integrating the contents of recollection into a cohesive memory representation. Several of the regions comprising the network have previously been reported to demonstrate age-related reduction in recollection-related activity (e.g., Daselaar et al., 2006; Kukolja et al., 2009; Tsukiura et al., 2010; Angel et al., 2013; Cansino et al., 2015).

The second component of retrieval processing examined here is 'retrieval monitoring'. This refers to control processes responsible for evaluating the outcome of a retrieval attempt in relation to behavioral goals (Burgess and Shallice, 1996; Rugg, 2004). The neural correlates of monitoring are identified by contrasting retrieval cues eliciting weak versus strong memory signals (e.g., Henson et al., 1999, 2000; Achim and Lepage, 2005; Wang et al., 2016). These prior studies have consistently implicated right dorsolateral prefrontal cortex (rDLPFC) and anterior cingulate cortex (ACC) in monitoring.

A relatively small number of fMRI studies have investigated the effects of age on the neural correlates of monitoring and, echoing findings from studies of recollection success, have yielded inconsistent results (see, for example, Duarte et al., 2010; Giovanello et al., 2010; Dulas and Duarte, 2014; Wang et al., 2016, for reports of null effects of age, and McDonough et al., 2013, and Mitchell et al., 2013, for reports of age-related impairment in monitoring-related activity in rDLPFC). Here, we examined whether fMRI 'monitoring effects' are sensitive not only to age, but also to individual differences in memory performance (cf. Wang et al., 2016).

Materials and methods

Data from the encoding phase of this experiment were reported in two prior publications (de Chastelaine et al., 2015, 2016), where additional description of the experimental procedures and methods can be found.

Participants

Thirty six young (18–29 yrs.; M = 22 yrs.; SD = 3.0 yrs.; 17 female), 36 middle-aged (43–55 yrs.; M = 49 yrs.; SD = 3.4 yrs.; 17 female) and