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Neural recruitment and connectivity during emotional memory retrieval across the adult life span

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ABSTRACT

Although research has identified age-related changes in neural recruitment during emotional memory encoding, it is unclear whether these differences extend to retrieval. In this study, participants engaged in a recognition task during a functional magnetic resonance imaging scan. They viewed neutral titles and indicated whether each title had been presented with an image during the study phase. Neural activity and connectivity during retrieval of titles associated with positive and negative images were compared with age (treated as a continuous variable) included as a regressor of interest. Aging was associated with increased prefrontal activation for retrieval of positive and negative memories, but this pattern was more widespread for negative memories. Aging also was associated with greater negative connectivity between a left hippocampal seed region and multiple regions of prefrontal cortex, but this effect of age occurred during negative retrieval only. These findings demonstrate that age-related changes in prefrontal recruitment and connectivity during retrieval depend on memory valence. The use of a life span approach also emphasized both continuities and discontinuities in recruitment and connectivity across the adult life span, highlighting the insights to be gained from using a full life span sample.

1. Introduction

Healthy aging, even in the absence of dementia, is associated with cognitive declines, including memory retrieval (Salthouse, 2011). However, it has been suggested that memory impairments in older adults can be mitigated by the presence of emotional arousal (Kensinger, 2009b). Critically, some studies have found that older adults' emotional enhancement is particularly strong when the information is of positive valence (Charles et al., 2003), suggesting that valence, and not only emotional arousal, can influence memory processes in healthy aging. This age-related enhancement of positive information has been of great interest in the cognitive aging literature, as it represents a special circumstance in which age-related cognitive declines may be reduced by specific task-related factors. Further, both young and older adults may process positive and negative information differently, with negative information associated with more visual processing and positive information associated with more conceptual processing (Kensinger, 2009b). As such, age-related changes to positive and negative event retrieval may reflect changes on a number of dimensions relevant to cognitive processing.

One important question that has emerged from the examination of emotional memory in healthy aging is how emotion may alter neural recruitment associated with specific mnemonic processes, and how these influences may differ as a function of age. Identifying the neural correlates of this effect could help researchers understand the underlying cognitive mechanisms contributing to emotional enhancement in older adults. Prior studies have suggested that healthy aging is associated with increased prefrontal cortex (PFC) activity during encoding of emotional relative to neutral information (see St Jacques et al., 2009a for review), and of positive relative to negative information (Leclerc and Kensinger, 2008). In addition to age-related differences in neural recruitment, previous studies have also identified age-related changes in neural connectivity during emotional encoding. Specifically, healthy aging influences connectivity within the medial temporal lobe (MTL) and between the MTL and PFC. Amygdala-hippocampal connections may be weakened in older adults during the encoding of negative information (St. Jacques et al., 2009b), and older adults show stronger connectivity between the hippocampus, amygdala, and mPFC during the encoding of positive information than do young adults (Addis et al., 2010). Age-related changes in neural activity and connectivity during emotional encoding have been

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explained as potentially revealing age-related shifts in self-referential processing, where older adults interpret positive stimuli in a more self-relevant way (Kensinger and Leclerc, 2009), as well as age-related increases in emotional regulation strategies in healthy older adults (St. Jacques et al., 2009b).

Although most research examining the effects of age on the neural correlates of emotional memory has focused on encoding processes, several behavioral studies suggest that healthy aging also has an effect on processes associated with retrieval. Specifically, older participants exhibit greater increases in ratings of positive valence for personal memories (Kennedy et al., 2004), even when the age of encoding is held constant, and they perceive their recall of positive events to be more vivid than negative ones (Petrican et al., 2008). Investigating the effect of emotional valence on the neural correlates of memory retrieval may elucidate the reasons for these differences. Previous studies have shown increased activity in the amygdala (Dolan et al., 2000; Murty et al., 2009; but see, Taylor et al., 1998) and lateral frontal lobes (Murty et al., 2009) during retrieval of emotional relative to neutral events, thought to reflect the retrieval of affective content or the reexperience of an affective response, and the monitoring and elaboration of the memory, respectively. However, the effect of valence and healthy aging on these processes is still unknown. The present study extends prior work by examining age-related changes in neural recruitment during retrieval of positive and negative information.

Behavioral studies of memory retrieval reveal linear declines in performance starting as early as in one's early 30s (Salthouse, 2011). Similarly, behavioral studies with continuous age designs suggest that age-related changes in emotional experience (Pasupathi and Carstensen, 2003) and emotional memory (Carstensen and Turk-Charles, 1994) may occur gradually over time. Despite this evidence, previous studies examining the effects of healthy aging on neural recruitment during memory tasks have often compared young adults (typically 18- to35-year-old) with older adults (often aged more than 60-year-old), ignoring individuals between the ages of 35 and 60 years. Therefore, it currently is unknown whether the neural changes of middle-aged adults are similar to those of older adults. In addition, while previous research has shown that the emotional valence can have opposite effects on neural recruitment in young and older adults (Leclerc and Kensinger, 2008), it is unknown whether this change is discrete (i.e., valence influences neural recruitment for young and middle-aged adults in the same way until a certain age, then this effect is reversed) or gradual (i.e., middle-aged adults exhibit a pattern of activity i.e., in-between that of young and older adults). To answer these questions, the present study uses a life span assessment to examine the effects of emotion on the memory network.

One potential difficulty with examining the neural activity associated with emotional episodic memory retrieval is that representing participants with studied emotional and neutral stimuli could lead to neural differences stemming from the processing of the retrieval cues, in addition to those related to remembering the encoding event. A number of recent functional magnetic resonance imaging (fMRI) studies have avoided this potential confound of on-line emotional processing by having participants encode a neutral item in a neutral or emotional study context and using the neutral item as the retrieval cue (Maratos et al., 2001; Sterpenich et al., 2006). This method helps ensure that valence differences at retrieval are related to the mnemonic content and not the retrieval cue. In the present study, we use a paradigm that has been reported previously (Ford et al., 2014), in which participants encode positive, negative, and neutral images presented with neutral titles. During a scanned retrieval session, participants view the neutral titles, to avoid confounds associated with an emotional retrieval cue, and retrieve the related emotional or neutral image.

The present study examines age-related changes in neural recruitment, particularly in prefrontal regions, and in MTL-PFC connectivity during retrieval of emotional events. Based on prior evidence that older adults shift to prefrontal rather than sensory based processing (Davis et al., 2008), we hypothesize that healthy aging will be associated with increased prefrontal and decreased posterior activation during successful retrieval. We are particularly interested in how emotional valence interacts with aging to influence prefrontal activity and connectivity. During encoding, healthy older adults recruit prefrontal regions to a greater extent during positive relative to negative events, whereas young adults exhibit the reverse activation pattern (i.e., negative > positive; Leclerc and Kensinger, 2008), and healthy aging is associated with increased MTL-PFC connectivity during encoding of positive events, but not negative (Addis et al., 2010). Similar age-related increases in prefrontal activity and connectivity during positive event retrieval would demonstrate that age-related changes in emotional processing seen during encoding extend to retrieval. Conversely, age-related changes in neural activity and connectivity that do not replicate these patterns would suggest that emotion influences distinct cognitive processes during encoding and retrieval.

2. Methods

2.1. Participants

Data from 63 healthy adults (mean age = 47.92 years, standard deviation [SD] = 19.80, ages 19–85 years; mean education = 16.56, SD = 2.34) are reported. The ratio of males to females was roughly one-to-one (30 females and 33 males) and was approximately equivalent within each decade (43%–67% male in each decade), with no significant difference in this distribution across decades ($x^2(6, N = 63) = 0.85$, $p = 0.99$). Twenty-seven of the young adult subjects from this sample were included in a recent article examining the interactive effects of emotional valence and memory phase on neural recruitment (Ford et al., 2014). Gender distribution was even across the age range and age was not significantly correlated with education ($p = 0.68$). Two additional participants were recruited but not scanned because of contraindications for fMRI (ages 50 and 75 years; both male). Another 10 participants were scanned, but were excluded from the current analysis because of equipment malfunction (n = 1; age = 49 years, education = 16 years, male), an abnormal structural scan (n = 1, age = 49 years, edu = 17, female), excessive motion (n = 1, age = 56 years, edu = 16, male), voluntary early termination of the MR session (n = 1, age = 49 years, edu = 14, female), or low behavioral performance (n = 6, mean age = 55.64, SD = 18.12, ages 30–83 years; mean education = 16.12, SD = 3.49; 2 female). Participants were right-handed native English speakers without psychiatric illness or neurologic disorder and were recruited from the greater Boston area. All participants were paid for their participation and gave written informed consent in accordance with the requirements of the Institutional Review Board at Boston College.

All participants completed the Beck Anxiety Inventory (Beck et al., 1988) to examine self-reported symptoms of anxiety, as well as the Beck Depression Inventory (Beck et al., 1961) and the Geriatric Depression Scale (Sheikh and Yesavage, 1986) to evaluate symptoms of depression. In addition, participants engaged in a series of tests intended to examine general cognitive ability, vocabulary, verbal fluency, working memory, and memory (both immediate and delayed). Finally, all participants completed a battery of cognitive tests implemented in CogState, a computerized neuropsychological test battery that was approximately 30 minutes in duration. The battery included 6 subtests that examine a range of cognitive abilities, including: Detection Task (speed of processing),