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Effective connectivity during successful and unsuccessful recollection in young and old adults

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ABSTRACT

Aging effects on regional brain activation have been studied extensively to explain the gradual recollection failure that occurs with advancing age. However, little is known about the consequence of aging on the interaction among brain regions that support recollection. The purpose of this study was to examine effective connectivity at encoding and retrieval during successful and unsuccessful recollection in young and old adults. In particular, we analyzed a recollection network that is characterized by its susceptibility to aging effects by middle age or later, which is comprised of the occipital cortex, hippocampus and orbitofrontal cortex. Participants' brains were scanned using functional magnetic resonance imaging while they performed a spatial source memory task. Dynamic causal modeling and Bayesian model selection revealed that subsequent recollection during encoding and recollection during retrieval modulated the influence of the orbitofrontal cortex on the hippocampus in both age groups; this particular connectivity was not modulated by unsuccessful encoding in either group. Successful encoding and retrieval of item-source associations modulated all connections within the network in old adults. The findings revealed that the orbitofrontal cortex influences processes in the hippocampus to ensure successful recollection, and aging alters the recollection network by engaging non-specialized connections.

1. Introduction

Aging is characterized by a dramatic decline in the ability to retrieve the details of our own experiences, such as the temporal or spatial information associated with episodes; however, recognizing that a previous event has been lived without any additional details is almost unaffected by age, as revealed by numerous studies (for a meta-analysis see Spencer and Raz (1995)). The former ability is referred to as recollection, whereas the latter is familiarity (Brown and Aggleton, 2001; Jacoby and Kelley, 1992; Mandler, 1980). Because these two processes are unevenly affected with advancing age, it is essential to examine each of them separately to understand the effects of age on episodic memory.

Several functional magnetic resonance imaging (fMRI) studies have adopted this approach to examine episodic memory encoding (e.g., Ankudowich et al., 2016; Cansino et al., 2015a; de Chastelaine et al., 2011; Dennis et al., 2008; Dulas and Duarte, 2011, 2014; Kukolja et al., 2009; Leshikar and Duarte, 2014; Mattson et al., 2014; Maillet and Rajah, 2016; Miller et al., 2008) and retrieval (e.g., Ankudowich et al., 2016; Cansino et al., 2015b; Duarte et al., 2008; Dulas and Duarte, 2012, 2014; Duverne et al., 2008; Kukolja et al., 2009; Leshikar and Duarte, 2014; McDonough et al., 2013, 2014; Mitchell et al., 2013) using source memory or associative recognition tasks, which allow the objective measurement of recollection. These studies have identified crucial brain regions that exhibited significant activation differences related to age. However, few studies (Addis et al., 2010; Daselaar et al., 2006; Dennis et al., 2008; Hampstead et al., 2016; Matthäus et al., 2012; Oedekoven et al., 2013; Oh and Jagust, 2013; St. Jacques et al., 2012; Wang et al., 2010; Waring et al., 2013; Ystad et al., 2010) have attempted to examine these regions at a system level, i.e., how these

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regions interact during episodic memory encoding and retrieval and whether these interactions differ with advancing age.

1.1. Effects of aging on neocortical connectivity during episodic memory

Age differences in episodic memory networks have mainly been assessed using functional connectivity procedures that do not provide directional information on the connectivity of the brain regions (Daselaar et al., 2006; Dennis et al., 2008; Matthäus et al., 2012; Oedekoven et al., 2013; Oh and Jagust, 2013; Wang et al., 2010; Ystad et al., 2010) and rarely by means of effective connectivity that allows the evaluation of the direction of influence between regions (Addis et al., 2010; Hampstead et al., 2016; St. Jacques et al., 2012; Waring et al., 2013). Several of these studies (Addis et al., 2010; Oedekoven et al., 2013; Oh and Jagust, 2013; Waring et al., 2013) focused on recognition tasks in which recollection and familiarity processes are mixed; two studies (Wang et al., 2010; Ystad et al., 2010) examined brain connectivity during the resting state to determine its relationship with memory performance.

The effects of age on recollection encoding networks have been examined through whole brain analyses using an associative recognition task (Dennis et al., 2008) and an object-location association task (Hampstead et al., 2016). The former study investigated the functional connectivity between the hippocampus and the rest of the brain and found that relative to young adults, old adults manifested stronger connectivity between the hippocampus and bilateral prefrontal regions (ventrolateral, superior, dorsolateral and orbitofrontal cortices) and lesser connectivity between the hippocampus and posterior regions (occipitotemporal and fusiform cortices). In the study by Hampstead et al. (2016), Granger causality analyses on 45 regions of interest (ROIs) were conducted on data from healthy old adults and patients with mild cognitive impairment. Their results revealed that healthy old adults had a left dominant network in encoding involving the inferior frontal, anterior intraparietal sulcus and posterior cingulate regions. Hampstead et al. (2016) also examined recollection networks during retrieval and found that the right hippocampus interacted with almost all of the ROIs. However, the effects of age on effective connectivity were not assessed in this study because young adults were not included.

Recollection retrieval networks have been examined in autobiographical memory (Matthäus et al., 2012; St. Jacques et al., 2012) and through quasi-exponential functions based on old/new recognition judgments and confidence rates (Daselaar et al., 2006). By conducting whole brain functional connectivity analyses, Matthäus et al. (2012) found that old adults increased their network density and size compared to young adults and showed connectivity between frontal and parietal regions that were not present in young adults. Specific networks were examined in two additional studies (St. Jacques et al., 2012; Daselaar et al., 2006). Using dynamic causal modeling (DCM), St. Jacques et al. (2012) found that the recollection of episodic details modulated the influence of the ventrolateral-prefrontal cortex on the hippocampus less in older adults compared with young adults. The functional connectivity analyses conducted by Daselaar et al. (2006) revealed that old adults showed greater connectivity between the rhinal cortex and bilateral prefrontal cortex, whereas young adults showed greater connectivity between the hippocampus and parieto-temporal regions.

Studies examining the effects of age on recollection using systems level analysis showed that the medial temporal lobe structures, in particular the hippocampus and several prefrontal cortices, are relevant during both encoding (Dennis et al., 2008) and retrieval (St. Jacques et al., 2012; Hampstead et al., 2016). During encoding, old adults exhibited stronger connectivity between the hippocampus and bilateral prefrontal cortices (Dennis et al., 2008), whereas during retrieval, both fewer (St Jacques et al., 2012; Daselaar et al., 2006) and more (Hampstead et al., 2016) interactions have been detected between these two brain regions. The participation of regions from the occipital cortex on recollection networks has been less systematically studied; old adults exhibited less connectivity between the hippocampus and bilateral occipital cortex during encoding (Dennis et al., 2008) and less connectivity within the occipital areas during retrieval (Matthäus et al., 2012).

1.2. The recollection network assessed in the current study

In previous experiments from our group (Cansino et al., 2015a, 2015b), we were concerned with detecting which brain regions exhibited the initial changes related to aging recollection decay in the adult lifespan. To answer this question, we conducted fMRI scans in young, middle-aged and old adults while they performed a spatial source memory paradigm. We found that during encoding only two regions showed changes in subsequent memory effects by middle age that continued until old age (Cansino et al., 2015a). These regions were the left medial orbitofrontal gyrus and the left superior occipital gyrus; in the former region, middle-aged and old adults, under-recruited activity relative to young adults, whereas activity was over-recruited in the superior occipital cortex. Conversely, during retrieval (Cansino et al., 2015b), no region showed any significant neurofunctional variation by middle age. However, relative to young adults, the brain activity of old adults was lower in the right superior orbitofrontal gyrus and bilateral hippocampus, among other regions. Although the activity in these regions in middle-aged adults did not differ significantly from the other two age groups, their activity clearly was situated between these two groups, suggesting a gradual under-recruitment of activity in these regions with advancing age.

Brain activity variations in the hippocampus, orbitofrontal cortex and occipital cortex related to recollection deficits as a consequence of age have been reported in other studies as well. In the hippocampus, activity was shown to be diminished in old adults compared to young adults during encoding (Dennis et al., 2008) and retrieval (Daselaar et al., 2006; Dulas and Duarte, 2014; Kukolja et al., 2009). Likewise, brain activity in the orbitofrontal cortex has been shown to decrease later in old age during item-source encoding (Dulas and Duarte, 2011). In the superior occipital cortex, results are mixed; Ankudowitch et al. (2016) found an activation increase in this region as a function of age in an adult lifespan sample in which encoding and retrieval data were jointly analyzed, as it was observed by middle-age with fMRI (Cansino et al., 2015a) and event-related potentials (Cansino et al., 2010). During retrieval, it has been observed that occipital cortex activity is under-recruited in old adults relative to young adults (Dulas and Duarte, 2012).

The functional contribution of the hippocampus, orbitofrontal cortex and superior occipital cortex for recollection has also been outlined. The hippocampus has been identified as the most critical structure that supports recollection at encoding and retrieval as revealed by numerous studies on patients with a hippocampal lesion (e.g., Giovanello et al., 2003; Turriziani et al., 2004) and fMRI studies (for a review see Diana et al. (2007)). During encoding, the hippocampus binds the elements from an experience into an episodic representation, allowing for its later recollection (Eichenbaum et al., 2007), whereas during retrieval, cues from previous experiences reactivate the episodic representation in the hippocampus, which in turn receives information support from the ventral and dorsal visual streams (Eichenbaum et al., 2012). The orbitofrontal cortex is essential in learning associative information according to studies in non-human (e.g., Meunier et al., 1997) and human (Duarte et al., 2010) primates. During retrieval, the role of the orbitofrontal cortex was uncovered by patients with focal damage in this region who showed an inability to accurately recall the contextual details of personal experiences, leading to confabulation symptoms (e.g., Gilboa et al., 2006; Schnider and Ptak, 1999). Confabulations and non-pathologic context misattributions observed in healthy individuals have been attributed to a failure of retrieval strategies that control recollection by constraining the memory search to