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Age-related changes in neural oscillations supporting context memory retrieval

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ABSTRACT

Recent evidence suggests that directing attention toward single item-context associations during encoding improves young and older adults' context memory performance and reduces demands on executive functions during retrieval. In everyday situations, there are many event features competing for our attention, and our ability to successfully recover those details may depend on our ability to ignore others. Failures of selective attention may contribute to older adults' context memory impairments. In the current electroencephalogram (EEG) study, we assessed the effects of age on processes supporting successful context memory retrieval of selectively attended features as indexed by neural oscillations. During encoding, young and older adults were directed to attend to a picture of an object and its relationship to one of two concurrently presented contextual details: a color or scene. At retrieval, we tested their memory for the object, its attended and unattended context features, and their confidence for both the attended and unattended features. Both groups showed greater memory for attended than unattended contextual features. However, older adults showed evidence of hyper-binding between attended and unattended context features while the young adults did not. EEG results in the theta band suggest that young and older adults recollect similar amounts of information but brain-behavior correlations suggest that this information was supportive of contextual memory performance, particularly for young adults. By contrast, sustained beta desynchronization, indicative of sensory reactivation and episodic reconstruction, was correlated with contextual memory performance for older adults only. We conclude that older adults' inhibition deficits during encoding reduced the selectivity of their contextual memories, which led to reliance on executive functions like episodic reconstruction to support successful memory retrieval.

1. Introduction

Healthy aging is commonly associated with declines in episodic memory (for review: Craik & Rose, 2012; Spencer & Raz, 1995). In studies of source or context memory (for review: Mitchell & Johnson, 2009; Spencer & Raz, 1995), where the memory for an item and a property of the item or initial encoding experience (e.g., location, orienting question, item

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color) are assessed (Johnson, Hashtroudi, & Lindsay, 1993), young adults outperform their older counterparts. This decline is found even when item memory is matched (James, Strunk, Arndt, & Duarte, 2016; Kensinger & Schacter, 2006; Mitchell & Johnson, 2009). Context memory is thought to rely on frontally mediated executive functions to a greater extent than item memory during encoding and retrieval (Mitchell & Johnson, 2009). This is consistent with evidence suggesting that aging is associated with greater declines in cognitive processes reliant on the prefrontal cortex (e.g., the frontal aging hypothesis) (West, 1996).

Emerging evidence suggests that explicitly instructing both younger and older adults to attend to the relationship between an item and its context increases memory for the item-context association in both groups (Dulas & Duarte, 2013, 2014; Glisky & Kong, 2008; Glisky, Rubin, & Davidson, 2001; Hashtroudi, Johnson, Vnek, & Ferguson, 1994; Kuo & Van Petten, 2006; Naveh-Benjamin, Brav, & Levy, 2007). For example, directing attention to an item-color association (e.g., "Is this a likely color for this item?") increases memory for that association over directing attention to the item alone (e.g., "Is this item smaller than a shoebox?") (Dulas & Duarte, 2013). One possible mechanism for the memory improvement is that explicit attention strengthens the relationship between the item and its context at encoding (Uncapher, Otten, & Rugg, 2006). Another, non-mutually exclusive possibility is that the strengthened relationship reduces demands on executive functions at retrieval (Cohn, Emrich, & Moscovitch, 2008; Kuo & Van Petten, 2006).

While many experimental tasks assess memory for an item and a single contextual feature, in the real world we are likely to have multiple features competing for our attention. The ability to recover these contextual features at retrieval is likely a product of where we directed our attention at encoding. The ability to selectively attend to relevant features and ignore the irrelevant features is reduced in older adults (Kim, Hasher, & Zacks, 2007). This reduction in selective attention is suggestive of reduced inhibitory control (Hasher & Zacks, 1988). A reduced ability to selectively attend to a specific relationship may lead older adults to hyper-bind (Campbell, Hasher, & Thomas, 2010) and show a conditional dependence (Boywitt, Kuhlmann, & Meiser, 2012; Meiser, Sattler, & Weisser, 2008; Peterson & Naveh-Benjamin, 2016; Starns & Hicks, 2008) between relevant and irrelevant features during memory retrieval. A consequence of hyper-binding, in typical memory tasks, may be an impoverished memory representation for relevant contextual features. This in turn may lead to increased demands on executive functions at retrieval, such as episodic reconstruction and post-retrieval monitoring, in order to make accurate context memory decisions.

In a previous event related potential (ERP) study from our lab (James et al., 2016) we investigated contextual memory in both young and older adults where, at encoding, we directed attention to the relationship between one of two presented contexts: a color and a scene. Participants were required to direct attention to the appropriate (i.e., attended) context and ignore the other (i.e., unattended) context. At retrieval, we tested their memory for both the attended and unattended context features. We found that both groups demonstrated better memory for the attended feature, suggesting they were able to selectively attend to the appropriate context during encoding. Older adults showed conditional dependence between the two contextual features, indicative of hyper-binding, which we concluded was due to a reduced ability to inhibit the unattended context at encoding. The FN400 and parietal old-new effects were found to be similar across age groups. The FN400 has been linked to familiarity-based memory (Duarte, Ranganath, Winward, Hayward, & Knight, 2004; for review: Friedman & Johnson, 2000; Rugg & Curran, 2007) and conceptual priming (Voss, Lucas, & Paller, 2009). The parietal-old new effect is associated with recollection-based memory (Curran, 2000; Friedman & Johnson, 2000; Wilding, 2000), and can be modulated by the amount of information recollected (Vilberg, Moosavi, & Rugg, 2006). The similarity of these effects suggests that both young and older adults had intact recollection and familiarity. We found differences between young and older adults in the late posterior negativity (LPN), in which a reliably larger LPN was found for the older adults, compared to the young adults. The LPN has been linked to episodic reconstruction of the encoding episode through reactivation of context-specifying information (Cycowicz, Friedman, & Snodgrass, 2001; Johansson & Mecklinger, 2003). We concluded that while young and older adults recollected a similar amount of information, more of this information was likely irrelevant with respect to context memory decisions for the older adults. Consequently, older adults relied on episodic reconstructive processes to a greater extent than the young in order to recover relevant contextual information.

The current study uses the data from our previous ERP study to investigate the relationships between aging and context retrieval, with neural oscillations. An advantage of investigating neural oscillations over ERPs, is that they are thought to represent both local and long range communication between cell assemblies and reflect the synchronized inhibitory and excitatory firing rates (Jacobs, Kahana, Ekstrom, & Fried, 2007; Lee, Simpson, Logothetis, & Rainer, 2005). These synchronized fluctuations are thought to be critical for both encoding and retrieval of long-term memory (for review: Axmacher, Mormann, Fernandez, Elger, & Fell, 2006; Duzel, Penny, & Burgess, 2010; Nyhus & Curran, 2010). Another advantage of investigating neural oscillations is that they may contain more information about the underling cognitive processes, as ERPs only reflect a summation of power across all frequencies, and only those that are phase locked (i.e., synchronize at the same time across all individual trials) (Makeig, Debener, Onton, & Delorme, 2004). The current study capitalizes on the additional information provided by neural oscillations to investigate age-related differences in contextual memory retrieval.

Neural oscillations are commonly grouped into specific frequency bands of interest, such as theta (4–7 Hz), alpha (8–12 Hz), and beta (12–30 Hz). Event related synchronization and desynchronization refers to an increase or decrease in power from a resting, or prestimulus, interval (Pfurtscheller & Aranibar, 1977). Both synchronization and desynchronization within these frequency bands have been shown to reflect memory performance during both encoding and retrieval (for review: Hanslmayr & Staudigl, 2014; Klimesch, 1999). Greater theta synchronization, indexed by greater mean power, for correctly identified old items compared to both forgotten items and correctly rejected new items, is consistently found within