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Visual integration enhances associative memory equally for young and older adults without reducing hippocampal encoding activation

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ABSTRACT

The ability to remember associations between previously unrelated pieces of information is often impaired in older adults (Naveh-Benjamin, 2000). Unitization, the process of creating a perceptually or semantically integrated representation that includes both items in an associative pair, attenuates age-related associative deficits (Bastin et al., 2013; Ahmad et al., 2015; Zheng et al., 2015). Compared to non-unitized pairs, unitized pairs may rely less on hippocampally-mediated binding associated with recollection, and more on familiarity-based processes mediated by perirhinal cortex (PRC) and parahippocampal cortex (PHC). While unitization of verbal materials improves associative memory in older adults, less is known about the impact of visual integration. The present study determined whether visual integration improves associative memory in older adults by minimizing the need for hippocampal (HC) recruitment and shifting encoding to non-hippocampal medial temporal structures, such as the PRC and PHC. Young and older adults were presented with a series of objects paired with naturalistic scenes while undergoing fMRI scanning, and were later given an associative memory test. Visual integration was varied by presenting the object either next to the scene (Separated condition) or visually integrated within the scene (Combined condition). Visual integration improved associative memory among young and older adults to a similar degree by increasing the hit rate for intact pairs, but without increasing false alarms for recombined pairs, suggesting enhanced recollection rather than increased reliance on familiarity. Also contrary to expectations, visual integration resulted in increased hippocampal activation in both age groups, along with increases in PRC and PHC activation. Activation in all three MTL regions predicted discrimination performance during the Separated condition in young adults, while only a marginal relationship between PRC activation and performance was observed during the Combined condition. Older adults showed less overall activation in MTL regions compared to young adults, and associative memory performance was most strongly predicted by prefrontal, rather than MTL, activation. We suggest that visual integration benefits both young and older adults similarly, and provides a special case of unitization that may be mediated by recollective, rather than familiarity-based encoding processes.

1. Introduction

Older adults often have difficulty with associative memory – the ability to remember associations between previously unrelated pieces of information (Naveh-Benjamin, 2000; reviewed in Old and Naveh-Benjamin (2008)). Age-related associative memory impairment in older adults relative to young adults has been observed across various types of stimuli, including word pairs (Naveh-Benjamin, 2000; Castel and Craik, 2003), words and fonts (Naveh-Benjamin, 2000, Experiment 3), words and scenes (Bayen, 2000), faces and names (Naveh-Benjamin et al., 2004), faces and locations or scenes (Bastin and Van der Linden, 2006; Dennis et al., 2008), objects and locations or colors (Chalfonte and Johnson, 1996), and picture pairs (Naveh-Benjamin et al., 2003).

Associative memory performance can be improved among older adults in several ways. The deficit, relative to young adults, is reduced when the stimulus pairs have a pre-existing semantic relationship, such as the word pair *Abdomen-Stomach* compared to an unrelated word pair like *Zero-Sad* (Naveh Benjamin et al., 2005; Patterson et al., 2009; Badham et al., 2012). Semantic relatedness may improve associative memory by narrowing down potential responses at retrieval and helping to reject unrelated lures (Badham et al., 2012). However, some exceptions exist. For example, Gutchess and Park (2009) found little influence of semantic-relatedness of object-scene pairs on performance in older adults.

Providing adults with explicit instructions to engage in elaborative encoding also boosts associative memory performance, for example, by

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creating a sentence that meaningfully links two words in a pair (Naveh-Benjamin et al., 2007), or by constructing a mental image that includes both items in a pair (Naveh-Benjamin et al., 2005). It is interesting to note that sometimes these elaborative strategies benefit only older adults (Naveh-Benjamin et al., 2007), but sometimes benefit both young and older adults equally (Naveh-Benjamin et al., 2005), preserving the overall age differences in associative memory performance between groups.

While elaborative encoding strategies may build a bridge between items, Parks and Yonelinas (2015) suggest that the optimal associative encoding strategy is one where two items are fully integrated or "chunked" so that they are encoded as a single unit rather than two linked, but still separate entities, a process they refer to as "unitization". The mnemonic benefit of unitization has been demonstrated with items that share a pre-existing unitized meaning, such as "GREEK-MYTHOLOGY" (Zheng et al., 2015) or words imagined in a relevant integrated color, such as "BALLOON" imagined in yellow (Diana et al., 2011). In addition, previously unrelated items can be unitized through an integrative sentence such as "CLOUD-LAWN: A yard used for sky-gazing" that seeks to combine the original meaning of both words to produce a single new meaning (Quamme et al., 2007) or by imagining an object in a previously unrelated color, such as "ELEPHANT" in red (Staresina and Davachi, 2006; Diana et al., 2011).

Like elaborative encoding, unitization attenuates age-related associative memory deficits (Bastin et al., 2013; Ahmad et al., 2015). The mnemonic benefit of unitization in older adults has been demonstrated with verbal stimuli including compound words (Bader et al., 2010; Zheng et al., 2015) and word-color pairs (Bastin et al., 2013). However, the mechanism underlying the effect is unclear. Unitization may decrease the degree to which strategic binding is necessary for subsequent successful associative recognition (Haskins et al., 2008), and at the same time may increase reliance on familiarity-based responding at retrieval (Bastin et al., 2013; Parks and Yonelinas, 2015) that has been shown to remain relatively intact in older adults compared to recollection (Daselaar et al., 2006).

While the benefits of unitization for older adults have been demonstrated with verbal stimuli, less is known about visual unitization. Most associative memory paradigms using visual stimuli have presented two items as separate entities on a black or white background, such as pictures of faces and tools placed side by side (Düzel et al., 2003), or pictures of faces and houses placed randomly on a black background (Piekema et al., 2010). In the real world, however, objects, faces, and houses are linked to one another within the broader visual context of the scene in which they are experienced. Objects and scenes, for example, are virtually always perceived in relation to one another, and thus may be inherently integrated. Multiple previous experiments in our laboratory have suggested that objects presented in a scene are integrated into a single unit, such that changes to the scene result in impaired recognition for the object (Hayes et al., 2007). Consistent with Gaffan (1994), we have argued that objects within a scene are processed relatively automatically as an integrated unit; they are not merely an object plus a scene.

The present study will investigate whether visual integration of objects and scenes has similar benefits for older adults as the semantic unitization manipulations used by Quamme et al. (2007) and Zheng et al. (2015). We predict that visually integrating an object within a scene will benefit older adults (and possibly young adults) on an associative memory task, relative to the more typical presentation of an object adjacent to its paired scene on a white background. Importantly, all the objects and scene pairs included in the study were strongly semantically related (such as a lamp in a living room) and the instructions to participants emphasized the elaborate encoding of each object with its unique scene, thus providing optimal circumstances for successful associative memory in older adults.

The study will also investigate the impact of visual integration on patterns of fMRI activation in cortical regions involved in visual associative memory. Associative memory is assumed to rely on interactions between medial temporal and prefrontal regions (Gaffan et al., 2002; Bunge et al., 2004; Barker and Warburton, 2015). In the medial temporal lobes, unimodal sensory association areas that process information about object qualities (the "what" pathway) serve as the primary input to the perirhinal cortex (PRC), which mediates the perception and representation of complex object-feature conjunctions (Barense et al., 2007; Ryan et al., 2012). Polymodal visual and spatial processing regions (the "where" pathway) project to the parahippocampal cortex (PHC) (Eichenbaum et al., 2007), presumably mediating the well-established role of PHC in visual-spatial associations and scene processing (Sommer et al., 2005; Davachi, 2006; Awipi and Davachi, 2008; Preston et al., 2010; Staresina et al., 2011). These two pathways converge in the hippocampus (HC), suggesting a unique role for the HC in binding objects with spatial locations (Squire et al., 2004), their contexts (Bar and Aminoff, 2003), and three-dimensional space (Mullally and Maguire, 2011).

Unitization may decrease reliance on hippocampally-mediated binding for successful subsequent associative memory. Several lines of evidence support this notion. First, amnesic patients with hypoxic damage limited to the HC show better associative memory for unitizable word pairs compared to pairs that are not easily unitized, suggesting that they may rely to a greater extent on extra-hippocampal structures for encoding unitized pairs (Quamme et al., 2007). Second, using ROC curves, Parks and Yonelinas (2015) demonstrated that memory for unitized pairs relied to a greater extent on familiarity during retrieval, compared to associated but not unitized pairs. Familiarity-based retrieval is thought to be dependent upon the PRC rather than the HC (Diana et al., 2007; Eichenbaum et al., 2007). Items that are later recognized based on familiarity show less hippocampal activation during encoding than items subsequently recognized based on recollection (Otten, 2007), but it is not clear whether PRC activation also increases during encoding of these items. To our knowledge, no study has compared directly the activation in the PRC and HC during encoding of unitized and non-unitized associative pairs.

In the present study, we predicted that encoding of visually integrated pairs relative to non-integrated pairs would show less activation in HC and increased activation in extra-hippocampal medial temporal lobe structures, such as the PRC. Alternatively, it is possible that objects embedded within scenes are processed simply as a "scene", thereby reducing the amount of activation in PRC and shifting the emphasis instead from HC to PHC.

This shift away from HC to other medial temporal lobe structures may be even more prominent for older adults, who tend to rely on familiarity-based responding more than young adults (Daselaar et al., 2006). Alternatively, older adults may rely to a greater degree than young adults on dorsolateral prefrontal cortex (DLPFC) and ventrolateral prefrontal cortex (VLPFC) for successful encoding. These regions show consistent fMRI activation during both associative encoding and associative recognition (Bunge et al., 2004; Park et al., 2012). VLPFC activation is thought to reflect the maintenance and rehearsal of information in working memory (Rypma and D'Esposito, 2000), whereas DLPFC activation may reflect the manipulation of information in working memory (Barbey et al., 2013). Both regions have been implicated in age-related compensation (Hayes et al., 2017; Erk et al., 2011; Cabeza et al., 2002). Thus, better associative memory may be observed in older adults who engage these regions to a greater degree during associative encoding.

In order to understand the impact of unitization on age-related associative memory and the cortical structures mediating unitization, we presented young and older adults with associative pairs of objects and naturalistic scenes while undergoing fMRI scanning. Objects were presented either visually integrated into a semantically related scene as they would be perceived in the real world (Combined condition), or objects and semantically related scenes were presented adjacent to one another on a white background (Separated condition), as depicted in