

available at www.sciencedirect.comwww.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****Age-effects on associative object–location memory**

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ABSTRACT

Aging is accompanied by an impairment of associative memory. The medial temporal lobe and fronto-striatal network, both involved in associative memory, are known to decline functionally and structurally with age, leading to the so-called associative binding deficit and the resource deficit. Because the MTL and fronto-striatal network interact, they might also be able to support each other. We therefore employed an episodic memory task probing memory for sequences of object–location associations, where the demand on self-initiated processing was manipulated during encoding: either all the objects were visible simultaneously (rich environmental support) or every object became visible transiently (poor environmental support). Following the concept of resource deficit, we hypothesised that the elderly probably have difficulty using their declarative memory system when demands on self-initiated processing are high (poor environmental support). Our behavioural study showed that only the young use the rich environmental support in a systematic way, by placing the objects next to each other. With the task adapted for fMRI, we found that elderly showed stronger activity than young subjects during retrieval of environmentally richly encoded information in the basal ganglia, thalamus, left middle temporal/fusiform gyrus and right medial temporal lobe (MTL). These results indicate that rich environmental support leads to recruitment of the declarative memory system in addition to the fronto-striatal network in elderly, while the young use more posterior brain regions likely related to imagery. We propose that elderly try to solve the task by additional recruitment of stimulus–response associations, which might partly compensate their limited attentional resources.

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1. Introduction

One of the most common memory complaints of elderly is that they are unable to remember the location of household objects, like keys (e.g. Jonker et al., 1996).

These complaints are part of an age-related episodic memory decline (for review, see Hedden and Gabrieli 2004), in particular of contextual memory. For instance, elderly show problems remembering which of two experimenters presented a target (McIntyre and Craik 1987, Schacter et al., 1994), what gender the presenter was (e.g. Simons et al., 2004), or what the target's case format was (e.g. Kausler and Puckett 1981) and what colour the target was presented in at study (Park and Puglisi 1985, see Spencer and Raz 1995 for a review). Given that item memory stays generally intact (Craik and McDowd 1987) (for a recent meta-analysis, see Old and Naveh-Benjamin 2008), it was hypothesised that elderly are impaired at binding contextual elements into a coherent episode, also called the associative deficit (Naveh-Benjamin 2000). Adding to the age-related associative deficit is the so-called resource deficit (Craik and Byrd 1982), which posits that a lack of cognitive, in particular attentional resources, makes it difficult to use self-initiated processes.

With age, several brain structures essential for self-initiated processes (the fronto-striatal network) and associative memory (the Medial Temporal Lobe; MTL) deteriorate structurally with age. Foremost, lateral prefrontal cortex volume decreases around 5% per decade, starting at age 20 (Raz et al., 2005, Resnick et al., 2003). Decline in the basal ganglia is also apparent, for instance, caudate volume declines with 0.75% per year (Raz et al., 2005). Similar decline is observed in the hippocampus (0.79%), but age-related degeneration of the frontal lobe is the most prominent.

Next to structural decline, also age-related functional decline is observed. For instance, the hippocampus, which is well known to be involved in encoding and retrieval of between-domain associations (Mayes et al., 2007), often shows decreased activation in elderly during encoding (e.g. Mitchell et al., 2000) and retrieval (e.g. Cabeza et al., 2004). Furthermore, elderly show reduced performance on several memory tasks, like cued recall (e.g. Craik and McDowd 1987), source memory (e.g. Wegesin et al., 2000) and associative memory (Chalfonte and Johnson 1996, Glisky et al., 2001, Naveh-Benjamin 2000; Naveh-Benjamin et al., 2003, 2004). Implicitly imposing strategic processing during encoding enhances source memory performance (Wegesin et al., 2000). However, explicitly imposing strategic processing during encoding and retrieval does not entirely eliminate the associative deficit (Naveh-Benjamin et al., 2007). This indicates elderly probably not only have problems with self-initiation (like implementing strategies), they might also be unable to optimally use the strategies that are offered to them (Dunlosky and Hertzog 1998).

The MTL and fronto-striatal network are known to interact with each other (e.g. Poldrack and Packard 2003, Poldrack and Rodriguez 2004). This has been observed in stimulus-response learning (Poldrack et al., 1999), but also in object-location associative memory (Iaria et al., 2003). Since the MTL and fronto-striatal network interact, they might also be able to

compensate for each other. This was for instance observed in patients with specific damage to the caudate nucleus by Voermans and colleagues (2004). They showed that activation of the right hippocampus compensated for gradual functional degradation of the caudate nucleus in a route recognition task. In healthy young adults, an increased interaction was found between the caudate and hippocampus. This indicates that the hippocampus can compensate for reduced caudate processing when necessary.

Here we aim to investigate if elderly show compensatory activity in the fronto-striatal network in an object-location associative memory retrieval task, where the demand on self-initiated processing is manipulated during encoding only. Following the concept of resource deficit, elderly probably have difficulty using their declarative memory system when demands on self-initiated processing are high, which can be established by offering little contextual information (or so-called environmental support (Craik et al., 1987)). The task used is the same as used by De Rover et al. (2008). They investigated self-initiated processes in an fMRI study using an episodic memory task for sequences of object–location associations in a grid. Here, the structure of the sequence during encoding could implicitly influence the representation used at retrieval. During encoding, either all the objects were visible simultaneously (rich environmental support) or every object became visible transiently (poor environmental support). They found that young adults adapted their representation used at retrieval to the encoding cues available. Rich environmental support during encoding rendered activation in regions related to mental imagery (Wheeler et al., 2000), such as the fusiform gyrus, the lingual gyrus and cuneus during retrieval, in addition to areas generally found active during retrieval tasks. In turn, poor environmental support during encoding rendered activation in the globus pallidus and thalamus during retrieval; structures that are generally involved in memory where temporal information is crucial (Ivry and Spencer 2004, Packard and Knowlton 2002, Vakil et al., 2000).

We hypothesise that elderly will not be able to use the environmental support as systematically as the young use it (imagery), due to a lack of attentional resources. To investigate if the elderly use the extra environmental support in the same systematic way as the young, we first conducted a complementary behavioural experiment with unconstrained response order during recall in young and elderly adults, in which the encoding conditions were identical to the ones used in the fMRI experiment, to make sure any differences between conditions during retrieval are exclusively attributable to differences occurring at encoding.

Participants had to encode sets of 9 object–location associations in a 3×3 grid while either a rich environmental encoding structure was provided (all objects visible simultaneously), or while a poor environmental encoding structure was provided (isolated objects becoming visible sequentially). At recall, participants were instructed to reconstruct the grid freely.

To investigate the neural basis of this hypothesised absence of visual imagery in elderly and the putative fronto-striatal support to the declarative memory system, we applied the same task as described above in an fMRI study with young and elderly participants. Besides large overlap in brain

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