

## Effects of aging on transient and sustained successful memory encoding activity

Nancy A. Dennis\*, Sander Daselaar, Roberto Cabeza

Center for Cognitive Neuroscience, Duke University, Box 90999, LSRC Building, Durham, NC 27705, USA

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### Abstract

Event-related fMRI studies have investigated age-related changes in encoding by identifying greater activity for items that are later remembered than for those that are forgotten (difference in memory, or Dm). The present study used hybrid blocked/event-related analyses to distinguish between *transient Dm* versus *sustained Dm*. Dm was identified as parametric increases in encoding activity as a function of a combined subsequent memory/confidence scale. Dm was measured in each trial (transient activity) and in blocks of eight trials (sustained activity). Transient Dm analyses showed age-related reductions in the left hippocampus but increases in left prefrontal cortex (PFC). Sustained Dm analyses showed age-related reductions in right PFC, but no region showing increased activity in older adults. These findings suggest that during semantic classification older adults show less spontaneous hippocampal-mediated encoding processes, but greater PFC-mediated semantic processes. Additionally, the decline in sustained Dm in PFC may involve age-related deficits in sustained attention that impact encoding processes. The results underscore the importance of investigating aging effects on both transient and sustained neural activity.

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### 1. Introduction

Memory for personally experienced past events, or episodic memory, is one of the cognitive functions most affected by aging [16]. Older adults' difficulties with episodic memory may reflect deficits occurring during the initial storage of the information (encoding), the maintaining of information (storage), as well as recovery of the stored information (retrieval). Behavioral studies that manipulated attention during these two phases suggest that encoding deficits play a major role in older adults' episodic memory deficits [1,15,27]. Unfortunately, it is difficult to isolate encoding from retrieval differences using behavioral paradigms. The ideal methods to investigate this issue are functional neuroimaging techniques, such as functional MRI (fMRI), which provide a measure of the effects of aging on encoding activity. Moreover, using event-related paradigms, these techniques

can isolate neural activity specifically associated with successful encoding processes and determine how this activity changes as a function of aging. This was the goal of the present study.

To isolate successful encoding activity, event-related fMRI studies have used the *subsequent memory paradigm* [37], which identifies brain regions showing greater study-phase activity for items that are remembered than for those that are forgotten in a subsequent memory test. The difference between remembered and forgotten items is known as difference in memory or Dm. In fMRI studies, Dm has usually been found in medial temporal lobe (MTL) and prefrontal cortex (PFC) regions (e.g., [5,19], e.g., [34,43,51]). To our knowledge, only two event-related fMRI studies have applied the subsequent memory paradigm to investigate the effects of aging on encoding processes. First, a word encoding study by Morcom et al. [33] found that both young and older adults showed Dm in left MTL and PFC regions, and that Dm activity in PFC regions was more bilateral in older adults. The latter finding is consistent with abundant evidence of

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\* Corresponding author. Tel.: +1 919 668 4767; fax: +1 919 681 0815.  
E-mail address: ndennis@duke.edu (N.A. Dennis).

increased bilaterality in older adults [11]. Second, a picture encoding study by Gutchess et al. [25] found that, compared to young adults, older adults showed reduced Dm in bilateral MTL regions but greater Dm in bilateral PFC regions. Thus, taken together, these studies suggest that older adults may show reduced Dm in MTL and increased Dm in PFC. According to Gutchess et al., additional PFC recruitment in older adults could help compensate for the deficits in MTL recruitment. Consistent with this idea, they found in older adults a negative correlation between encoding activity in these two regions.

However, older adults do not always show greater encoding-related PFC activity than younger adults. Actually, several studies using positron emission tomography (PET) found age-related decreases in encoding activity in left and right PFC regions [1,8,24]. An important difference between these earlier PET studies and the recent fMRI studies described above is that the former used blocked designs, which are sensitive to both transient (trial-related) and sustained (blocked-related) activity, whereas the latter used event-related designs, which measure mainly transient activity. Thus, a potential explanation of inconsistent PFC findings is that, compared with younger adults, older adults show increased transient activity but decreased sustained activity. One possibility is that older adults are successful in engaging certain cognitive processes in response to the specific demands of each trial, but unsuccessful in sustaining attention throughout the whole encoding block. This hypothesis fits with the notion that *environmental support* attenuates age-related cognitive decline [17]: the concrete task performed in each trial guides processing, whereas maintaining attention throughout the task is more dependent on self-initiated processing. Moreover, when the encoding task requires semantic retrieval, which is a cognitive function relatively well preserved in older adults (e.g., [40]), older adults may rely on

this preserved ability and recruit PFC regions that partly compensate for MTL deficits. In contrast, sustained attention is a cognitive function significantly impaired in old age [32,38], and this deficit could have contributed to the age-related PFC decreases observed in blocked PET studies. To investigate the hypothesis that, during encoding, older adults show compensatory recruitment of transient PFC activity but deficits in sustained PFC activity we conducted a subsequent memory fMRI study using a hybrid event-related/blocked analysis.

Several fMRI studies have used hybrid event-related/blocked designs to distinguish transient versus sustained activity [7,20,36,50]. The typical method is to separate blocks of trials by an inter-block fixation period, in order to allow block-related analyses, and, simultaneously separate the trials within each blocked by jittered inter-trial fixation intervals, in order to allow trial-related analyses (see Fig. 1A). fMRI data is typically analyzed using the general linear model (GLM) that include regressors for the blocks as well as regressors for the trials, and that compares block-related activity to the inter-block fixation baseline and trial-related activity to the inter-trial fixation baseline. Although inter-block fixation intervals are critical if one wishes to compare memory-related block activity to a non-memory baseline, they are not necessary when the focus is on a “tighter” memory-related contrast. Thus, because we were interested in changes in activity as a function of subsequent memory, we eliminated inter-block intervals, and included only jittered inter-trial intervals, as in a standard event-related paradigm (see Fig. 1B). Thus, in our study the term hybrid applies specifically to the GLM analyses, which included both block and trial regressors. The block regressors corresponded to groups of eight trials.

Another innovation in our subsequent memory paradigm is that instead of coding each encoding trial as either remembered or forgotten, we measured both accuracy and confidence at test and scored each encoding trial in a three-level

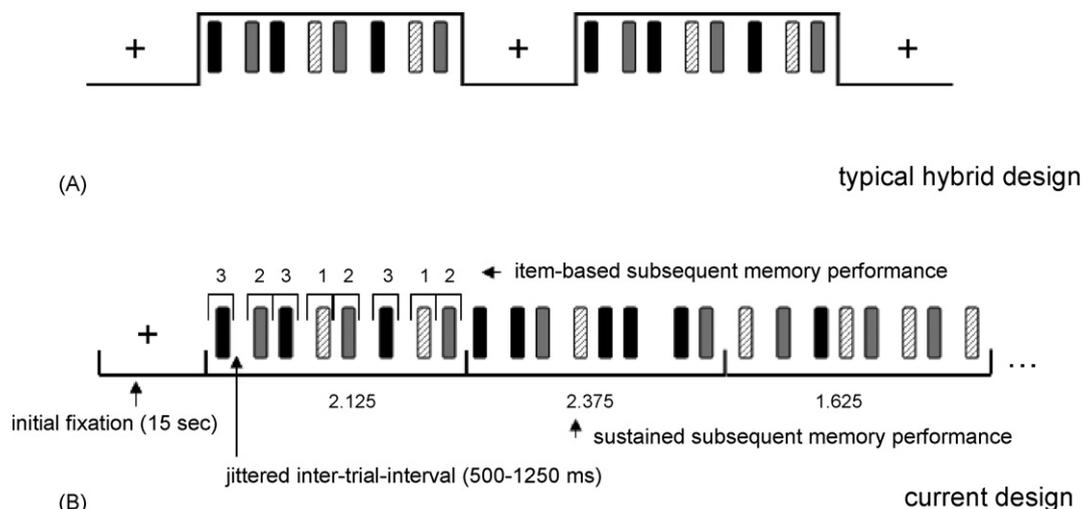


Fig. 1. A typical hybrid design (A) compares individual trials to a resting baseline state. Whereas our hybrid design (B), excludes the resting baseline condition, a condition that is not necessary in subsequent memory analysis. Rather, it separates trials into contiguous blocks (of eight in this case). Furthermore, trials are coded both individually based upon their subsequent memory score and as a block, based upon the average subsequent memory score of all individual trials within that block.

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