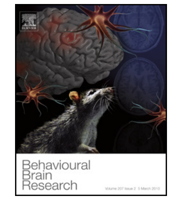
Behavioural Brain Research 280 (2015) 24–35

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr



Research report

fMRI subsequent source memory effects in young, middle-aged and old adults

Selene Cansino [a,*], Cinthya Estrada-Manilla [a], Patricia Trejo-Morales [a], Erick Humberto Pasaye-Alcaraz [b], Erika Aguilar-Castañeda [c], Perla Salgado-Lujambio [d], Ana Luisa Sosa-Ortiz [e]

[a] *Laboratory of NeuroCognition, Faculty of Psychology, National Autonomous University of Mexico, Mexico City, Mexico*
[b] *Institute of Neurobiology, National Autonomous University of Mexico, Querétaro, Mexico*
[c] *Cognition and Behavior Unity, National Institute of Neurology and Neurosurgery, Mexico City, Mexico*
[d] *Department of Neuroimaging, National Institute of Neurology and Neurosurgery, Mexico City, Mexico*
[e] *Laboratory of Dementias, National Institute of Neurology and Neurosurgery, Mexico City, Mexico*

HIGHLIGHTS

- We examine positive and negative subsequent source memory effects across the lifespan.
- We identified brain activity changes that occur in middle age during source encoding.
- Medial orbitofrontal gyrus during source encoding was under-recruited by middle age.
- Occipital superior gyrus during source encoding was over-recruited by middle age.

ARTICLE INFO

Article history:
Received 24 August 2014
Received in revised form
22 November 2014
Accepted 25 November 2014
Available online 2 December 2014

Keywords:
Episodic memory
Source memory
Subsequent memory effect
Aging
Functional magnetic resonance imaging

ABSTRACT

The ability to remember the spatial context in which our experiences occur declines linearly across the adult lifespan. However, little is known about whether this source memory decline is associated with neural activity changes. In the present study, functional magnetic resonance imaging (fMRI) scans were recorded in young, middle-aged and old adults to investigate brain activity variations across the adult lifespan during encoding of subsequent spatial source memory retrieval. Twelve healthy individuals of both sexes were enrolled in each age group. During encoding, participants performed natural/artificial judgment of images of common objects that were randomly presented in one of the quadrants of the screen. During retrieval, the images presented at encoding were randomly mixed with new ones and displayed at the center of the screen. Participants judged whether each image was new or old and, if an image was old, they were instructed to indicate in which quadrant the image was presented in the encoding session. The contrast between study items that were later recognized and assigned a correct source judgment with those whose sources were subsequently forgotten revealed that positive subsequent memory effects disappear by middle age in the left medial orbitofrontal gyrus and appear in the left superior occipital gyrus. This under-recruitment and over-recruitment brain activity was also present in old adults. The results allowed us to identify the specific brain regions that first fail to encode spatial information into an episodic representation during the adult lifespan.

1. Introduction

The memory of our own experiences that are comprised of multiple events and the contexts in which they occur is denominated by episodic memory [1]. This type of memory is highly vulnerable to the effects of aging. The effects are observed when individuals need to make use of recollection processes to retrieve events and contextual details but not when they employ familiarity processes that

* Corresponding author at: Laboratorio de NeuroCognición, Facultad de Psicología, Universidad Nacional Autónoma de México, Avenida Universidad 3004, Col. Copilco Universidad, Building D, Second Floor, Room 12, México, DF, 04510, Mexico. Tel.: +52 55 56 22 23 39; fax: +52 55 56 16 07 78.
E-mail address: selene@unam.mx (S. Cansino).

http://dx.doi.org/10.1016/j.bbr.2014.11.042
0166-4328/

only identify that certain information has been previously experienced without any additional information [2,3].

Source memory tasks that consist of retrieving the specific context in which different stimuli were encoded during study are suitable for evaluating recollection because they provide an objective method for assessing whether individuals are capable of retrieving the critical context under examination, which is unambiguous evidence that recollection processes are occurring. Because recollection is the underlying process that is seriously affected by age, it is crucial to use these types of tasks to assess the neural correlates related to episodic memory decline. In particular, there is evidence that spatial source memory, a context that is inherent to all episodic experiences, declines linearly with advancing age across the adult life span [4]. However, whether this linear decline is also associated with gradual brain activity changes is still unknown because source memory functional magnetic resonance imaging (fMRI) studies have only examined groups of extreme ages, i.e., young and old adults. The assessment of middle-aged adults as well constitute an essential approach to investigating when in adulthood brain activity changes start to occur and to estimate whether these changes are intermediate between those of the other two extreme age groups, suggesting a gradual modification of the neural resources responsible for recollection.

Additionally, neurophysiological techniques, such as fMRI or event related potentials (ERP), provide the valuable opportunity to examine whether changes in brain activity in middle-age occur when source information is encoded or during retrieval, or in both phases. In particular, during encoding, the analysis of subsequent source memory effects allows the determination of whether source memory decline is associated with inefficient memory formation. Two previous fMRI studies [5,6] on episodic memory have included middle-aged adults; however, both studies employed recognition tasks in which familiarity and recollection are likely mixed.

In the study by [5], brain activity during encoding and recognition was analyzed to determine their common correlations with age. Positive subsequent memory effects (recognized versus forgotten stimuli) and negative subsequent memory effects (forgotten versus recognized stimuli) were examined in the study by Park [6]. The former were characterized by age-related activity decreases in the occipital, temporal and parietal regions that were evident by middle-age, whereas negative subsequent memory effects were associated with increased activity with age in the superior medial frontal lobe and the posterior cingulated cortex by middle-age, and in the superior frontal lobe and angular gyrus in old-age.

Based on the studies that have included only groups of extreme ages to investigate subsequent memory effects using fMRI to predict recollection, two procedures have been used: source memory tasks [7–9] and associative recognition tasks [10–12]. However, there is still controversy surrounding whether this latter procedure relies exclusively on recollection [3], or on both recollection and familiarity [13,14].

Brain activity related to successful encoding varies across these studies; some of them observed under-recruitment activity in the fusiform gyrus [7,12] and the inferior temporal gyrus [12] in old adults relative to young adults. Additionally, over-recruitment activity in old adults has been recorded in the left [11,12] and right [11] prefrontal regions. Age effects on positive subsequent memory effects have been interpreted as the inability to allocate sufficient activity from brain regions relevant to memory encoding (under-recruitment) [15] or as the engagement of activity from additional brain regions (over-recruitment), not necessarily specialized in memory encoding, to compensate for neurofunctional age-decline [16] or due to the selection of inappropriate brain regions [17].

However, a notable and more consistent result across studies has been the lack of age effects on positive subsequent memory effects recorded in regions that are crucial for memory encoding, such as the bilateral hippocampus [8,11,12] and the left inferior frontal gyrus [8,11]; however, Dennis et al. [10] demonstrated age effects in these brain areas. These age-invariant results have broadened the search for other possible explanations of age-related encoding failure. Of particular interest are the intriguing results obtained when negative subsequent memory effects are examined because they are difficult to construe.

In associative recognition tasks, young adults compared to old adults showed larger negative subsequent memory effects in the bilateral precuneus [12], temporal cortex [11,12], and the prefrontal, occipital, parietal and posterior cingulate cortices [11]. However, based on a source memory task, negative subsequent memory effects were equivalent across age groups in several regions (e.g., the middle frontal gyrus, insula, cingulate cortex and supramarginal gyrus) [9]; however, [7] demonstrated age differences in the anterior cingulate cortex.

Because most of the brain regions showing negative subsequent memory effects coincide with those that have been identified as the “default mode network” [18], these effects have been interpreted as evidence that the structures of this network have been deactivated. The default mode network showed greater activation at rest in young adults, but it deactivates when resources are allocated to perform a cognitive task that requires the focus of attention on either external or internal information [19]. Therefore, because older adults exhibit less negative subsequent memory effects than young adults, it has been suggested that old adults experience difficulties with switching off the default mode network to allocate resources to accomplish memory formation tasks.

However, this interpretation has been challenged by some recent findings. For example, negative subsequent memory effects has also been recorded in regions that do not belong to the default mode network as the anterior insula and frontal operculum [9], regions that even have been identified as belonging to a “salience network” that initiates cognitive functions when a salient event occurs [20]. Moreover, negative subsequent memory effects showed consistent age differences in item recognition tasks [21–23] and associative recognition tasks [11,12] but not in source memory tasks [9]. The reason underlying why the default mode network was unaffected by age during the encoding of source information is unclear given that even less demanding tasks showed age effects. Further research is needed to confirm these findings.

The first aim of the present study was to investigate whether brain activity underlying successful source memory encoding starts to change by middle-age or whether these modifications occur only in old-age. If changes occur by middle-age, a second aim was to identify the first brain regions that show these neurofunctional variations in the adult life span and those that manifest changes until old-age and, in particular, to establish whether these changes occur in brain regions considered relevant for source memory encoding, such as the hippocampus and inferior frontal gyrus, or in regions that are not considered to be specialized for these processes. Finally, a third aim was to investigate whether negative subsequent memory effects show age-related variations by middle-age or only in late adulthood and to provide further evidence to elucidate whether these effects are observed exclusively in regions identified as the default mode network, such as the medial frontal and cingulated cortices, or whether they also manifest in regions distinguished by being responsible for other cognitive functions.

To achieve these goals, young, middle-aged and old adults were scanned using fMRI while they performed a source memory paradigm [24]. The paradigm consisted of presenting color images of common objects in one of four possible spatial locations during encoding (Fig. 1). During retrieval, participants indicated whether each image was new or old and, if an image was old, in which location it was presented at encoding. This procedure has the advantage of providing enough power to contrast subsequently recognized