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Age-related changes in neural activity during source memory encoding in young, middle-aged and elderly adults

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ABSTRACT

Source memory, the ability to remember contextual information present at the moment an event occurs, declines gradually during normal aging. The present study addressed whether source memory decline is related to changes in neural activity during encoding across age. Event-related potentials (ERPs) were recorded in three groups of 14 subjects each: young (21–26 years), middle-aged (50–55 years) and older adults (70–77 years). ERPs were recorded while the subjects performed a natural/artificial judgment on images of common objects that were presented randomly in one of the quadrants of the screen (encoding phase). At retrieval, old images mixed with new ones were presented at the center of the screen and the subjects judged whether each image was new or old and, if old, were asked to indicate at which position of the screen the image was presented in the encoding session. The neurophysiological activity recorded during encoding was segregated for the study items according to whether their context was correctly retrieved or not, so as to search for subsequent memory effects (SME). These effects, which consisted of larger amplitude for items subsequently attracting a correct source judgment than an incorrect one, were observed in the three groups, but their onset was delayed across the age groups. The amplitude of the SME was similar across age groups at the frontal and central electrode sites, but was manifested more at the posterior sites in middle-aged and older adults, suggesting that source memory decline may be related to less efficient encoding mechanisms.

1. Introduction

Recollection of the spatial–temporal context surrounding previous experiences or events progressively deteriorates with advancing age (Spencer & Raz, 1995), whereas recognition of the event itself is relatively unaltered in the elderly when it is evaluated by means of a recognition memory task in which the subjects have to indicate if a stimulus has been previously presented or not (e.g., Craik & McDowd, 1987). The context and the event constitute the memory of our own experiences that is termed as episodic memory (Tulving, 1972). Although episodic memory might be retrieved without the context information that took place when the event was encoded, a lack of contextual information renders a weak remembrance of the episode; this lack affects the quality and quantity of the information available in the elderly. The retrieval of episodic information with and without contextual information is designated as 'recollection' and 'familiarity', respectively.

Episodic memory deficits in the elderly have been attributed to incipient encoding processes. According to the level of processing (LOP) framework (Craik & Lockhart, 1972), memory performance reflects the initial mechanisms used to encode information. Events that are deeply semantically processed are more likely to be remembered than those that receive a shallow sensorial, structural or phonological processing (Craik & Tulving, 1975). Besides the nature of the encoding process, the amount of resources available for that process is also relevant. Aged people experience a reduction in processing resources that might result in less elaborate encoding operations and fewer conceptual associations with pre-existing knowledge (Craik, 2007). This proposal is based on the fact that semantic encoding strategies benefited memory performance more in young adults than in old subjects (Erber, Herman, & Botwinick, 1980; Simon, 1979). This lack of benefit has also been observed for source memory (remembering the speaker's voice) (Naveh-Benjamin & Craik, 1996), which indicates that the inability to use deep encoding strategies affects memory for item and context information equally.

Neurophysiological techniques allow evaluation of whether encoding deficits observed with aging in behavioral studies are related to neurofunctional changes. In particular, event-related potentials (ERPs) provide a high temporal resolution of brain activity recorded in real-time. The encoding processes can be measured

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by means of 'subsequent memory effects' (SME), which are measured by comparing brain activity for items that are later recognized successfully with brain activity for non-recognized items. Numerous studies have demonstrated that this method provides reliable evidence of neurophysiologic encoding processes (for reviews see Friedman & Johnson, 2000; Rugg, 1995).

The majority of ERP studies investigating SME in elderly subjects have based their analyses on recognition tasks in which the subjects were requested to indicate whether an item has been previously presented ('old') or not ('new') (Gutchess, Leuji, & Federmeier, 2007; Téllez-Alanís & Cansino, 2004). In these studies, memory was evaluated either under incidental conditions, in which, during encoding, the subjects did not know that their memory would be tested (Gutchess et al., 2007; Téllez-Alanís & Cansino, 2004) or under intentional conditions (Téllez-Alanís & Cansino, 2004). Subsequent memory effects were observed in the elderly under both incidental (Gutchess et al., 2007; Téllez-Alanís & Cansino, 2004) and intentional conditions (Téllez-Alanís & Cansino, 2004). However, SME differed between old and young subjects in only one of these experiments (Téllez-Alanís & Cansino, 2004).

The lack of consistent results in these studies may be due to the fact that all based their measurements of SME on recognition tasks in which both 'familiarity' and 'recollection' processes are present. However, the contribution of each of these processes to individual subjects' ability to provide a correct recognition response is unknown. To study the neural correlates of ineffective encoding processes in the elderly, it seems essential to use a memory task capable of distinguishing 'familiarity' from 'recollection', because, as has been mentioned, the memory for the item and its context in episodic memory are differently affected with aging. One previous study has used this approach (Friedman & Trott, 2000); in that study, the subjects learned two lists of sentences and were instructed to memorize the nouns and the list in which they appeared for a following memory test. SME were analyzed according to the subjects' performance in the 'Remember-Know' procedure (Tulving, 1985) and in a source memory paradigm. Both tasks assess 'familiarity' and 'recollection', but the first relies on subjects' subjective introspection, while the second objectively measures recollection for the context attribute under evaluation. In the 'Remember-Know' task subjects are requested to judge an item as 'remember' if they are able to retrieve any contextual information related to that item when it was first presented at study, or as 'know' if the item seems to them familiar but contextual information is not available. The source memory task used by Friedman and Trott (2000) consisted of the subject's indicating in which list (first or second) he or she had seen each noun presented at the study. The analysis of SME based on the comparison between 'remember' and 'know' responses or between subsequent correct and incorrect source responses permitted the isolation of brain activity actually related to the encoding of contextual information, and thus, of subsequent recollection processes, which are the most affected in the elderly. In this study, SME were observed in the 'Remember-Know' procedure but not in the source memory task. Young adults showed SME for both familiarity ('know' vs. missed judgments) and recollection ('remember' vs. 'know' judgments) processes, but old adults showed SME only for familiarity processes. This result is in agreement with evidence from behavioral studies (e.g., Cansino, 2009; Craik & McDowd, 1987), that familiarity processes are mostly preserved with advancing age.

Results from only one study are, however, insufficient to allow a definitive determination of whether encoding processes for subsequent 'recollection' as revealed by SME are dissimilar between young and elderly adults, especially since SME were observed in only one memory task when both applied tasks were assumed to assess the same memory processes. In addition, SME have been detected in young subjects (Cansino & Trejo-Morales, 2008) by means of a source memory paradigm similar to that employed by Friedman and Trott (2000).

The purpose of the present study was to determine whether brain activity during encoding for subsequent 'recollection' differs between young, middle-aged and old adults. Source memory deficit has usually been considered an impairment that appears late in life. The majority of the studies that have investigated this issue compared groups of young adults, usually under 30 years of age, with old adults, typically above 60 years of age (e.g., Glisky, Rubin, & Davidson, 2001; Schacter, Kaszniak, Kihlstrom, & Valdiserri, 1991) and did not include information about source memory performance during middle-age. However, there is evidence that source memory decay begins as early as after 31 years of age, since subjects between 31 and 40 years old performed significantly less well than subjects between 21 and 30 years old on a task assessing this parameter (Cansino, 2009). If 'recollection' or source memory impairment with advancing age is related to inefficient encoding processes, we expect that at encoding, the amplitude difference between the items whose sources are subsequently retrieved and those whose sources are subsequently forgotten (SME) will be of greater magnitude in young subjects than in middle-aged subjects, and of greater magnitude in the latter group than in old subjects. This amplitude difference for source memory performance should decrease across age groups, because there is evidence suggesting that SME reflect the strength or depth of the encoding process, with those items that are more intensely processed being more likely to be subsequently retrieved (for a review see Johnson, 1995). If, with advancing age, fewer resources are available during encoding, as stated by the LOP framework hypothesis (Craik, 2007), a reduction in SME with increasing age is expected. Another aim of the current study is to establish whether SME change temporally across the three age groups, since there is broad evidence suggesting a generalized slowing of cognitive processing with advancing age (Salthouse, 1996).

In this study, 'recollection' will be measured using the paradigm introduced by Cansino, Maquet, Dolan, and Rugg (2002) in a previous functional magnetic resonance (fMRI) study. This task reduces the probability that a correct source judgment could arise by chance from $P = 0.50$ to $P = 0.25$ by using a four-choice source memory task instead of the more conventional two-choice procedure. Only young adults participated in this fMRI study (Cansino et al., 2002) and SME were also assessed. The most prominent region showing these effects was observed in the right lateral occipital cortex. The activity in this region was interpreted as evidence that the items and their context which received greater perceptual processing were more likely to be successfully encoded into episodic memory.

Neuroimaging studies have consistently identified as relevant for episodic encoding brain activity recorded at prefrontal (e.g., Otten, Henson, & Rugg, 2001; Wagner et al., 1998) and medial temporal regions (e.g., Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Kirchhoff, Wagner, Maril, & Stern, 2000). In particular, left prefrontal activity has been associated with the encoding of verbal information while bilateral frontal activity has been observed for processing of information associated with images or pictures (e.g., Golby et al., 2001; Kelley et al., 1998). These results have been interpreted as evidence that two distinct codes, verbal and visual, are used to encode these types of stimuli (Paivio & Csapo, 1973). Moreover, the two source memory studies in young adults (Cansino & Trejo-Morales, 2008; Duarte, Ranganath, Winward, Hayward, & Knight, 2004), which used images as stimuli to search for recollection SME using the ERP technique, recorded these effects mainly at bilateral frontal sites. In the current study, we expect bilateral activity at the anterior electrode sites because we used rich and distinctive color images of common objects as stimuli.

Neuroimaging studies that have investigated age-related effects during the encoding of pictorial stimuli have reported similar brain