

Brain regions associated with successful and unsuccessful retrieval of verbal episodic memory as revealed by divided attention

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Received 8 November 2004; accepted 16 November 2004

Abstract

Which brain regions are implicated when words are retrieved under divided attention, and what does this tell us about attentional and memory processes needed for retrieval? To address these questions we used fMRI to examine brain regions associated with auditory recognition performed under full and divided attention (DA). We asked young adults to encode words presented auditorily under full attention (FA), and following this, asked them to recognize studied words while in the scanner. Attention was divided at retrieval by asking participants to perform either an animacy task to words, or odd-digit identification task to numbers presented visually, concurrently with the recognition task. Retrieval was disrupted significantly by the word-, but not number-based concurrent task. A corresponding decrease in brain activity was observed in right hippocampus, bilateral parietal cortex, and left precuneus, thus demonstrating, for the first time, involvement of these regions in recognition under DA at retrieval. Increases in activation of left prefrontal cortex (PFC), associated with phonological processing, were observed in the word- compared to number-based DA condition. Results suggest that the medial temporal lobe (MTL) and neo-cortical components of retrieval, believed to form the basis of episodic memory traces, are disrupted when phonological processing regions in left PFC are engaged simultaneously by another task. Results also support a component–process model of retrieval which posits that MTL-mediated retrieval does not compete for general cognitive resources but does compete for specific structural representations.

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Keywords: Recognition; Dual-task; Neuroimaging; Interference; Memory trace; Resources

1. Brain regions associated with successful and unsuccessful retrieval of verbal episodic memory as revealed by divided attention

Manipulating attention by having participants engage in two attention-demanding tasks simultaneously can be used to determine which memory processes draw on cognitive resources for their operation, and to incorporate that knowledge into theories of memory. Dividing attention has been shown to affect encoding much more than retrieval, leading researchers to conclude that the former, and not the latter, requires a general attentional system for optimal performance (Anderson,

Craik, & Naveh-Benjamin, 1998; Baddeley, Lewis, Eldridge, & Thomson, 1984; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Fernandes & Moscovitch, 2000; Naveh-Benjamin, Craik, Guez, & Dori, 1998). In line with these behavioural findings, neuroimaging studies have shown that neural activation in the prefrontal cortex (PFC) is reduced by dividing attention during encoding (Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Kensinger, Clarke, & Corkin, 2003; Shallice et al., 1994), but not during retrieval (Iidaka et al.).

However, recent behavioural research suggests that large disruptions in episodic memory also can occur from divided attention (DA) conditions at retrieval, specifically when the concurrent task uses material, and/or processing, similar to that used in the memory task. For example, a decrement in verbal memory of about 30% from full attention levels is observed when the concurrent task is word-based, whereas an

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equally demanding digit-based, or picture-based, task produces a decrement of only 10–15% (Fernandes & Moscovitch, 2000, 2002, 2003). Unlike the general effect observed from DA at encoding, which produces an approximate 50% decline in subsequent memory performance, across numerous types of distracting tasks, effects from DA at retrieval depend on the material or type of processing required in the distracting task. In this study, we use fMRI to examine the neural basis of the interference effect at retrieval, and consider the relevance of those findings for theories of memory.

It has been proposed that the large interference effects from DA at retrieval occur primarily as a result of competition for neo-cortical representations, which likely code phonology (Fernandes & Moscovitch, 2003; Fernandes, Priselac, & Moscovitch, 2005; Moscovitch, Fernandes, & Troyer, 2001). The present experiment tests this hypothesis and, in addition, highlights other brain regions that may be implicated. Differences in activation between those DA conditions that affect retrieval (i.e. word-based distracting task), and those that do not (digit-based distracting task), are expected in neocortical sites associated with verbal representation (semantic, orthographical and/or phonological), as well as in medial temporal lobe (MTL) and related structures associated with reactivation of the memory trace.

An alternative account is that large memory costs at retrieval result from competition for general attentional resources. Such resources, believed to be mediated by dorsolateral PFC, are needed to coordinate the online processing of dual-tasks (Anderson et al., 2000; Craik, 2001; D'Esposito et al., 1995; Iidaka et al., 2000), which may be more difficult as the similarity increases, between materials, and/or processing, in the distracting and memory tasks. This idea is consistent with Baddeley's (1992) hypothesis that the ability to coordinate concurrent tasks relies on the central executive (CE) of his working memory model, whose operation requires resources mediated by the PFC. If true, greater activation should be observed in dorsolateral PFC when attention is divided than full, and specifically, it should be greater when materials and/or processing requirements in the distracting task are similar (word-based) to that in the memory task, than different (digit-based distracting task). fMRI allows us to test these hypotheses, and to identify the brain regions associated with varying levels of proficiency of auditory recognition, during full and divided attention conditions.

2. Materials and methods

2.1. Participants

Twelve normal healthy participants (seven female; two left-handed), from 20 to 30 years of age (mean age = 26.33, S.D. = 3.36), with a mean of 16.5 years (S.D. = 2.33) of education completed the study after giving informed consent. All procedures were approved by a joint ethics committee of the University of Toronto, and the Baycrest Centre for Geriatric

Care. All participants spoke English fluently, and were free from psychiatric or neurological disease.

2.2. Behavioural task materials

All word stimuli, for the recognition and animacy tasks, were medium to high frequency words chosen from Francis and Kucera (1982). Word frequencies ranged from 20 to 100 occurrences per million. For each of the four study phases, participants heard a list of 50 unrelated words while in the scanner, presented at a rate of 1 word every 2 s. Encoding was not scanned.

During the recognition task, words were presented auditorily at a rate of 1 every 2 s, through Avotec headphones, and participants made a button-press to "old" words only. In each block, half of the words were old; these were presented pseudo-randomly throughout each block. Volume of presentation was adjusted individually for each participant, prior to the study phase, such that items could be heard over the noise produced by the scanner.

Items in the distracting tasks were presented visually at a rate of 1 every 2 s, on a white background, with black lettering or numbering, shown centrally through Avotec goggles adjusted for the acuity of each participant. The animacy task consisted of visual presentation of words with a mean of six letters, representing animals (e.g. kitten) and man-made objects (e.g. hammer). Participants responded when the visually presented word represented a non-living object. Stimuli for the odd-digit task consisted of visual presentation of two-digit numbers flanked by two Xs on either side, chosen from a table of random numbers (Kirk, 1995). Participants responded when the visually presented digit was odd. In each block, half of the items were targets requiring a button-press; these were presented pseudo-randomly throughout each block.

For the auditory baseline task, participants heard either the word "word" or "press", and made a button-press for the latter. In the visual baseline task, either a string of "OOOOOO" or "XXXXXX" was seen and participants made a button-press to the latter. For all tasks involving auditory presentation, participants responded by pressing a button with the index finger of the left hand, and for all tasks involving visual presentation responses were made with the right index finger, using two fMRI-compatible response pads (Lightwave Technologies, Surrey, BC, Canada).

2.3. Study procedure

Stimulus presentation and response recording were controlled by an IBM PC, using E-Prime v.1.0 software (Psychology Software Tools Inc., Pittsburgh, PA). Participants performed a practice session, outside of the scanner, consisting of a block of each task, and also a block for each of the dual-task conditions. They also performed a sample run in which blocks were presented randomly, as in the scanner. For each block in the practice and scanner session, 10 items were presented at a rate of 1 item every 2 s, preceded by 4 s

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