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Common prefrontal activations during working memory, episodic memory, and semantic memory

Lars Nyberg [a,*], Petter Marklund [a], Jonas Persson [a], Roberto Cabeza [b], Christian Forkstam [c], Karl Magnus Petersson [c], Martin Ingvar [c]

[a] *Department of Psychology, Umeå University, S-901 87 Umeå, Sweden*
[b] *Center for Cognitive Neuroscience, Duke University, Durham, USA*
[c] *Department of Clinical Neuroscience, Karolinska Institutet, Stockholm, Sweden*

Abstract

Regions of the prefrontal cortex (PFC) are typically activated in many different cognitive functions. In most studies, the focus has been on the role of specific PFC regions in specific cognitive domains, but more recently similarities in PFC activations across cognitive domains have been stressed. Such similarities may suggest that a region mediates a common function across a variety of cognitive tasks. In this study, we compared the activation patterns associated with tests of working memory, semantic memory and episodic memory. The results converged on a general involvement of four regions across memory tests. These were located in left frontopolar cortex, left mid-ventrolateral PFC, left mid-dorsolateral PFC and dorsal anterior cingulate cortex. These findings provide evidence that some PFC regions are engaged during many different memory tests. The findings are discussed in relation to theories about the functional contribution of the PFC regions and the architecture of memory.

Keywords: Prefrontal cortex; Memory; Positron emission tomography; Commonalities

1. Introduction

Functional brain imaging with positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have revealed a strong association between cognitive operations and activity in regions of the prefrontal cortex (PFC). For example, in a review of PET and fMRI studies [6], PFC regions were found to be part of the typical activation pattern for many different cognitive functions, including sustained attention, smell perception, written word recognition, verbal and spatial working memory, semantic memory, episodic memory, and conceptual priming.

In most prior studies, the focus has been on the role of specific PFC regions in specific cognitive domains. However, more recently it has been noted that regionally specific PFC activations show substantial similarities *across* cognitive domains [8,26]. In one recent analysis, Duncan and Owen [17] focused on five cognitive demands: response conflict, task novelty, number of elements in working memory, working-memory delay, and perceptual difficulty. They found that there was joint recruitment of three PFC regions for all five cognitive demands: mid-dorsolateral PFC, mid-ventrolateral PFC, and a dorsal part of the anterior cingulate cortex. These regions were seen as forming a common network recruited by as diverse challenges as response selection, working memory maintenance and stimulus recognition. It was furthermore noted that retrieval from episodic memory also tends to engage the same regions, and, in addition, that episodic retrieval showed a higher proportion of activations close to the frontal pole. These observations indicated that the common network is operating during episodic retrieval, but that additional processing associated with more anterior PFC regions also come into play.

The results from a recent fMRI study that directly contrasted working memory and episodic memory provide support for specific activation of frontopolar regions during episodic retrieval [7]. In contrast, another recent within-study fMRI comparison of working memory and episodic memory suggested that frontopolar activation was greater for working memory than for episodic memory [2], and frontopolar activation has also been associated with semantic monitoring [23]. Furthermore, both fMRI-studies [2,7] found evidence that dorsolateral PFC activation was stronger for working memory than for episodic memory.

* Corresponding author. Tel.: +46-90-7866429; fax: +46-90-7866695.
E-mail address: lars.nyberg@psy.umu.se (L. Nyberg).

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Thus, it is unclear whether dorsolateral PFC is engaged to a similar extent for different memory systems, and whether frontopolar activation is especially salient for episodic memory retrieval. At least in part, the unclear issues may have to do with different strategies for data analysis (between- versus within-study comparisons) and with factors that are task specific.

The aim of the present study was to further explore similarities in regionally specific activations associated with different memory systems. This was accomplished by analysis of data from two PET experiments [27]. Across the two experiments, three tests were included for each of three memory systems: episodic memory, working memory, and semantic memory. This design allowed analysis of regional activations that are common for a wide range of memory tasks.

2. Methods

2.1. Experimental tasks

The tasks that were used for the three systems are summarized in Table 1. Working memory was measured with 1- and 2-back tasks [3] and with a random-number generation task (cf. [32]). In the 1- and 2-back tasks, subjects were instructed that a sequence of words was to be presented and that their task was to decide for each word whether it was the same as the one presented one or two items earlier in the list. In the random-number generation task, subjects were instructed that each time a "?" appeared on the screen their task was to randomly generate a number between 1 and 10. They were told not to mention the same number twice in succession and to use all numbers between 1 and 10 before starting over again.

Episodic memory was measured with yes/no recognition (e.g. [28]), category-instance cued recall [36], and autobiographical memory [11]. In the recognition test, subjects were shown a mixed list of nine non-studied words and nine words from an intentional encoding session and were asked to say "yes" when they recognized a word and "no" when they thought a non-studied word was presented. In the cued-recall test, subjects were presented cue words (e.g. AUTHOR) and were asked to recall targets (e.g. STRINDBERG) from a previous study session (or say "no" if they could not recall the target). In the autobiographical test, subjects were presented cue words (e.g. VACATION) and were asked to use these for remembering personal events that could be related to each cue. They responded by saying one word that described their memory (e.g. "GREECE") or "no" if they could not come up with a personal memory.

Semantic memory was measured with living/non-living classification [19] fact retrieval (cf. [36]), and synonym generation (cf. [20]). In the living/non-living task, subjects were presented a list of words and decided if the words referred to living or non-living things. In fact retrieval, subjects were shown a series of cue words (e.g. AUTHOR) and were asked to retrieve factual information associated with each cue. They responded by saying one word that related to the factual information (or said "no"). In synonym generation, subjects were presented a series of words. For each word they were instructed to generate a different word with similar meaning (e.g. VACATION—HOLIDAY) or with a strong semantic association to the cue word (e.g. CAR—VOLVO).

The experiments also included a baseline reading condition. Subjects were told that a series of words was going to be presented and that their task was to read each word aloud. They were explicitly told that these words were not part of any test and that they did not have to memorize them.

2.2. Experimental procedure

The procedure for stimulus presentation and responding was the same for all tasks, and involved presentation of single items on a computer screen placed above the subjects' heads and responding by saying one word per stimulus (stimuli were words in all conditions except for random-number generation in which a series of "?" was presented). The presentation rate was 3 s (inter-stimulus interval = 2 s). Each experimental condition included 18 stimuli, 12 of which were presented during the scan interval.

Both experiments included seven experimental conditions, each presented and scanned twice (i.e. 14 scans/experiment). Experiment 1 included the following tasks: 2-back, random-number generation, recognition, cued recall, living/non-living, fact retrieval, and the baseline reading condition. Experiment 2 included: 1-back, cued recall, autobiographical memory, fact retrieval, synonym generation, and the reading baseline (a second baseline condition was also included but will not be considered here). The experimental tasks were presented in a counterbalanced order across subjects with the restriction that all conditions were performed before the replications were presented. An experimenter recorded the verbal responses (accuracy was >90% in all tasks).

Table 1
Experimental tasks

System	Task		
Working memory	1-Back	2-Back	Random-number generation
Episodic memory	Yes/no recognition	Category cued recall	Autobiographical memory
Semantic memory	Living/non-living	Fact retrieval	Synonym generation