



Dynamic switching between semantic and episodic memory systems

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ARTICLE INFO

Article history:

Received 4 March 2008

Received in revised form 17 November 2008

Accepted 30 November 2008

Available online 6 December 2008

Keywords:

Memory
Episodic
Prefrontal
fMRI
Learning

ABSTRACT

It has been suggested that episodic and semantic long-term memory systems interact during retrieval. Here we examined the flexibility of memory retrieval in an associative task taxing memories of different strength, assumed to differentially engage episodic and semantic memory. Healthy volunteers were pre-trained on a set of 36 face–name pairs over a 6-week period. Another set of 36 items was shown only once during the same time period. About 3 months after the training period all items were presented in a randomly intermixed order in an event-related fMRI study of face–name memory. Once presented items differentially activated anterior cingulate cortex and a right prefrontal region that previously have been associated with episodic retrieval mode. High-familiar items were associated with stronger activation of posterior cortices and a left frontal region. These findings fit a model of memory retrieval by which early processes determine, on a trial-by-trial basis, if the task can be solved by the default semantic system. If not, there is a dynamic shift to cognitive control processes that guide retrieval from episodic memory.

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1. Introduction

Retrieval from long-term memory is likely to employ constant interaction between different memory systems (Poldrack et al., 2001) to ensure smooth progression towards successful recovery of stored information which is relevant to the current goals. The interaction between memory systems, as well as brain networks supporting them, is dynamically changing on basis of factors such as rehearsal of the information and level of experience with the task (Chein & Schneider, 2005; Poldrack, 2000).

An everyday example of such a dynamic change is recalling the person-specific information, such as names, of persons whom we have previously encountered. Retrieving the names of familiar persons is a seemingly effortless process, whereas correctly naming persons met only once may involve effortful memory search to evoke the contextual details from the past encounter. Of course, familiar persons were once also unknown, which points to a fundamental learning-related re-organization of that information.

One way of conceptualizing such a learning-related re-organization is in terms of episodic and semantic memory (Tulving, 2002). Episodic memory is concerned with encoding, storage, and retrieval of personally experienced events, whereas semantic memory refers to general knowledge about the surrounding

world. Although still a matter of controversy, current theories seem to converge on the notion that repeated acquisition of the same information results in a change in how the episodic and semantic memory systems are involved (see Graham, Patterson, & Hodges, 1999; Moscovitch et al., 2005; Squire & Alvarez, 1995; Tulving, 2001). In the case of the above example, retrieving the name of a once met person would likely engage the episodic system, whereas retrieving the names of highly familiar persons can be based on the semantic memory system (i.e., there is no need to think back at a specific prior event). Support for this position comes from a cluster analysis (Dritschel, Williams, Baddeley, & Nimmo-Smith, 1992) which revealed a dissociation among retrieval of personal episodes (such as names of once met persons), personal semantic information (such as familiar names), and nonpersonal semantic information (such as names of presidents). Furthermore, a multivariate analysis of brain-imaging data (Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002) revealed that what could be conceived of as a test of personal semantic information (the autobiographical cued word-retrieval task) activated a similar left prefrontal network as factual retrieval, and was differentiated from activations associated with episodic memory (cued recall of experimental items). These findings suggest that one basis for a learning-related re-organization in case of associative recall, such as recalling someone's name, is that retrieval of well-learned associations engages the semantic memory system instead of the episodic memory system.

Episodic memory has been found to engage a specific network of prefrontal regions, its most characteristic feature being acti-

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vations in right inferior frontal and frontopolar cortices (Düzel et al., 1999; Habib, Nyberg, & Tulving, 2003; Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). These brain regions have been suggested to support *retrieval mode* (REMO), a neurocognitive task set that is a necessary precondition for episodic retrieval (Lepage, Ghaffar, Nyberg, & Tulving, 2000; Nyberg et al., 1995). REMO is hypothesized to be initiated by intention or instruction to retrieve information from one's personal past and maintained throughout the retrieval task, allowing stimuli to be treated as retrieval cues, suppressing irrelevant processing, and allowing successfully reactivated memory traces to be consciously attended to. By this definition, REMO activity should be present whenever episodic retrieval occurs, independently of retrieval success. Hence, to the extent that learning an association induces a shift from episodic to semantic memory, one would expect right prefrontal regions to be more engaged for relatively less familiar compared to more familiar items, regardless of whether the memory is actually retrieved. Conversely, strengthening of associations may induce increased activity in specific regions concerned with storage of that particular information during recall. Consistent with this notion, the recall of person-related semantic information (see Bruce & Young, 1986; Gobbini & Haxby, 2007) has been associated with lateral temporal (e.g., Elfgren et al., 2006; Gorno-Tempini & Price, 2001; Leveroni et al., 2000; Paller et al., 2003; Reinkemeier, Markowitsch, Rauch, & Kessler, 1997; Sergent & Signoret, 1992; Sugiura et al., 2006; Tsukiura, Mochizuki-Kawai, & Fujii, 2005), medial parietal (e.g., Elfgren et al., 2006; Shah et al., 2001; Sugiura et al., 2006), as well as medial temporal regions, including more anterior sites in or near the hippocampus and more posterior sites in the fusiform gyrus (e.g., Elfgren et al., 2006; George et al., 1999).

The main purpose of the present functional magnetic resonance imaging (fMRI) study was to test the notion of a selective role of REMO-specific regions in retrieval of "episodic" associations by examining functional brain activity during memory for weak and strong face–name associations. During a 6-week pre-fMRI training period, the participants were familiarized with a set of initially unfamiliar face–name associations. Half of the stimuli were shown only once (1×) over the entire training period and the remaining half was shown six times (6×), thereby introducing two levels of strength for the face–name associations. During fMRI scanning, 1× and 6× items were presented in randomly intermixed order in an event-related design to test for dynamic switching between semantic and episodic memory systems. We assumed that right prefrontal activation would be elicited in the 1× condition but not in the 6× condition. The reduction of right prefrontal activity was predicted to be most salient for hits in the 6× condition, which would be strongly dependent on semantic memory system; whereas right prefrontal involvement in the 1× condition was expected to be unaffected by retrieval success (Nyberg et al., 1995, 2000). A secondary purpose was to examine learning-related increases in brain activity, with a special focus on posterior association cortices, which would be consistent with increased involvement of semantic memory system with repeated learning.

2. Methods

2.1. Subjects

The study included 16 healthy young adults who participated as volunteers and received a monetary reward corresponding in value to 100 USD. Twelve of these participants were included in the fMRI part of the study (five females, seven males; mean age 19.3 years). All subjects were right-handed and had normal or corrected-to-normal visual acuity. The study was approved by the ethics committee at the University Hospital of Northern Sweden.

2.2. Materials

The items were 72 colour photographs of young adults (equal number of male and female faces) previously unseen by the participants. The photographs featured

a person's head and neck on identical grey background. Visible clothing details were masked. All persons depicted on photographs had a neutral facial expression.

2.3. Procedure

The study consisted of a training period of 6 weeks, followed by brain imaging with fMRI. Each training week consisted of two sessions (Fig. 1).

On the first session, the participants were shown 42 face–name pairs on a computer screen, each pair consisting of a photograph and a first name under it. Of the 42 items presented, 36 were repeated each week (6× items) and 6 were new on each week (1× items). The items were shown on a screen at a rate of one item per 8 s, with no pause between the items. The division of items into 1× and 6× conditions was fixed across subjects.

On the second session, occurring later the same week, the participants underwent a forced-choice recognition test on the 42 items presented previously that week. During the recognition task, a photo was presented with four names depicted under it, all with the same initial letter. The stimuli were presented at a rate of 8 s, with no pause between items. The task was to pick the correct name from the four alternatives. Response accuracy during the testing sessions was recorded.

The fMRI testing occurred 3 months after the last training week. Two weeks before the fMRI testing, subjects were presented the 36 6× items one additional time in a booster session. The task during the fMRI testing was identical to the test session during the training period: a forced-choice recognition task among four alternative names for each face. The stimulus duration was 2500 ms. The presentation of the stimuli was randomly alternated between 36 1× items, 36 6× items and 36 "null events", i.e., 2500 ms long presentations of fixation crosses. The latter events were included to induce a variation in inter-trial intervals between recognition items, which is necessary for analysis of rapid event-related designs (Burock, Buckner, Woldorff, Rosen, & Dale, 1998).

2.4. fMRI data acquisition

Functional magnetic resonance imaging was conducted on a 1.5T Philips Intera scanner (Philips Medical Systems, Netherlands). Blood-oxygen-level-dependent (BOLD) contrast T2*-weighted images were collected using a gradient echo-planar (EPI) sequence. The sequence had the following parameters: echo time 50 ms, flip angle 90°, TR 3000 ms, 33 transaxial slices acquired, slice thickness 4.4 mm.

Subjects viewed the stimuli through a tilted mirror attached to the head coil and gave their responses using four fingers of the right hand on a response pad, corresponding to the four alternative answers. To minimize the scanner noise, headphones were used, and to minimize head movement, cushions inside the head coil were used. Presentation of the stimuli and registration of responses was done using E-Prime 1.1 (Psychology Software Tools Inc., PA, USA). Response accuracy and reaction time were recorded.

2.5. Data analysis

Functional imaging data were preprocessed using the SPM2 software (Wellcome Department of Cognitive Neurology, London, UK). All visualisation of statistical maps and BOLD signal changes was done using in-house developed software (*Data Z*).

All images were preprocessed in a number of steps before statistical analysis: realignment, unwarping, correction for variability in slice acquisition timing, normalization to an EPI template in the MNI space, and smoothing with 8-mm FWHM Gaussian kernel.

The data was analysed in the framework of the general linear model. Both correct and noncorrect as well as missing answers were included in the analysis. The reason for including functional activation corresponding to stimuli with missing answers was the assumption that despite a missing answer, subjects were still engaged in task-relevant processing (i.e., retrieval mode for 1× items). In a first-order analysis, the subjects' responses were modelled as delta functions corresponding to the response moment (when an answer was given) or stimulus onset (for missing answers), convolved with hemodynamic response function. The different stimulus types (1× and 6×) were modelled separately for correct, incorrect, and missing answers. The null events were treated as baseline and not modelled explicitly. Second-order analysis over all subjects was performed, treating subjects as random effects.

The following contrasts were estimated. First we computed the simple main effect of experimental condition (1× or 6×) relative to the baseline condition. Statistical maps were thresholded at the level of $p < .001$, uncorrected, with an extent threshold of 20 voxels. The results obtained from these contrasts were then used as an inclusive mask ($p < .01$) for subsequent analyses of differential activations in the 1× and 6× conditions.

An additional, post hoc analysis was performed to test for the possibility that the differences in the prefrontal activation in 1× and 6× conditions arose from different levels of mental effort as indexed by significant differences in reaction times (Table 1). The conditions were modelled at the single subject level as above, with an additional regressor involving all trials. The additional regressor was parametrically modulated with reaction time data corresponding to each of the events (for missing answers, mean of each subjects' reaction times was used). On the second level analysis, the effect corresponding to reaction time was calculated and

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