Control of Semantic Interference in Episodic Memory Retrieval Is Associated With an Anterior Cingulate-Prefrontal Activation Pattern

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Abstract: Prefrontal activation is a consistent finding in functional neuroimaging studies of episodic memory retrieval. In the present study we aimed at a further analysis of prefrontal neural systems involved in the executive control of context-specific properties in episodic memory retrieval using an event-related fMRI design. Nine subjects were asked to learn two 20-item word lists that consisted of concrete nouns assigned to four semantic categories. Ten items of both word lists referred to the same semantic category. Subjects were instructed to determine whether nouns displayed in random order corresponded to the first 20-item target list. The interference evoked by the retrieval of semantically related items of the second list resulted in significantly longer reaction times compared to the noninterference condition. Contrasting the interference against the noninterference retrieval condition demonstrated an activation pattern that comprised a right anterior cingulate and frontal opercular area and a left-lateralized dorsolateral prefrontal region. Trial averaged time series revealed that the PFC areas were selectively activated at the interference condition and did not respond to the familiarity of learned words. These findings suggest a functionally separable role of prefrontal cortical areas mediating processes associated with the executive control of interfering context information in episodic memory retrieval. *Hum. Brain Mapping* 13:94–103, 2001. © 2001 Wiley-Liss, Inc.

INTRODUCTION

The control of interference induced by competing information-processing streams is a significant com-

ponent of executive control processes in memory retrieval. The prefrontal cortex (PFC) is considered to play a major role in strategic and evaluative processes of cognitive performance and a considerable number of functional imaging studies repeatedly demonstrated PFC activation in episodic memory formation and memory retrieval [Buckner et al., 1996; Nyberg et al., 1996; Henson et al., 1999a; Düzel et al., 1999; Wagner et al., 1998a; Fletcher et al., 1998; Lepage et al., 1999]. However, the functional interpretation of these

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PFC activation patterns remains largely unclear. Theoretical approaches to the PFC contribution to memory retrieval were often framed in terms of retrieval success [Rugg et al., 1996; Buckner et al., 1998a], retrieval effort [Schacter et al., 1996a], or retrieval attempt [Nyberg et al., 1995]. Although these functional interpretations gave a heuristic framework of experimental procedures designed to investigate a variety of hypotheses on PFC activation patterns during memory retrieval, the appropriateness of the simple dichotomy of success versus attempt or effort has been questioned.

Henson and colleagues [1999a] proposed a different approach based on the theoretical assumptions of a multistage model of episodic memory retrieval [Schacter et al., 1998]. According to this approach, PFC activity in episodic memory retrieval is related to the inherent monitoring demands of the task. The authors introduced a word recognition paradigm consisting of two word lists that differed only in whether task solution required reference to the spatiotemporal context of items learned during a previous encoding period. Their results suggested a dissociation of ventral and dorsal right hemisphere PFC areas that were supposed to subserve “cue specification” and “information monitoring”, respectively. Further evidence for the hypothesis that PFC activation patterns in memory retrieval processing primarily reflect the executive demands of the recognition task was provided by Wagner and colleagues [1998a]. The results of that study demonstrated a higher engagement of anterior and dorsolateral PFC areas in conditions where the discrimination between old and novel stimuli did require reference to the retrieval context. In the present study we aimed at further differentiating the functional significance of PFC activation in episodic memory retrieval. We specifically focused on the significance of context information by constructing an experimental procedure in which the episodic memory retrieval conditions were varied by the degree of interference in information processing. Hitherto, the involvement of brain areas in inhibitory processing or conflict resolution has only been studied in the working memory domain using Stroop or Stroop-like tasks [Carter et al., 1995, 2000; Bush et al., 1998] or n-back tasks evoking interference by recency effects [D’Esposito et al., 1999a]. These studies of interference control (also referred to as interference resolution [D’Esposito et al., 1999a]) showed different PFC activation patterns that were supposed to subserve the executive demands of conflict resolution in working memory. We hypothesized that the evaluation and resolution of competing information-processing

streams evoked by the semantic relationship of verbal stimulus material will engage a monitoring process in episodic memory retrieval. Therefore, we developed a semantic interference control paradigm that allows for the direct contrast of interfering and noninterfering retrieval conditions. This experimental paradigm offered the opportunity to selectively identify brain areas that might play a specific role in the control of semantic interference in episodic memory retrieval.

MATERIALS AND METHODS

Subjects

We investigated nine right-handed healthy volunteers (4 male, 5 female, mean age: 24.5 years, range: 20–30 years) who were recruited from students and medical staff of the Magdeburg University Faculty of Medicine. No subject had a history of neurological or psychiatric disorders or received any type of medication possibly interfering with cognitive performance. Informed and written consent was obtained from all participants.

Development of the task

The experimental procedure we used in a pilot study consisted of a word-list learning period and a delayed recognition task. Subjects were instructed to learn first a 20-item word list (target list) and immediately thereafter a second 20-item word list (distractor list), both to 100% criterion. The items of each list consisted of concrete nouns that were assigned to six semantic categories (animals, fruits, musical instruments, vegetables, kitchenware, and beverages), two of which (animals, fruits) were the same in the target list and distractor list. The items of the two word lists did not differ with respect to their relative frequency in German language (frequency analysis was based on the corpus of the Institute of German Language freely available on the internet at <http://corpora.ids-mannheim.de/~cosmas/>). In the pilot study, items from the target list and distractor list, as well as novel semantically unrelated items, were presented on a computer screen. The presentation time was 0.5 s followed by a 3.5 s interstimulus interval (ISI), during which a fixation cross appeared on the screen. Subjects were instructed to determine whether the item displayed on the computer screen was part of the target list and to respond as quickly as possible with a button press. In all cases where the presented stimulus matched with a target list item, subjects were instructed to use the left-hand index finger for a “yes”

response and in all other cases the left-hand middle finger for a “no” response. The recognition task followed the learning period with a short time delay. It was divided into five experimental sessions each consisting of the pseudorandomized presentation of 20 target-list items, 20 distractor-list items, and 40 novel items that were not related to the semantic categories of the previous word lists. Thus, a total of 400 items was presented during five sessions separated by 2-min rest periods. For the analysis of the behavioral data all trials were assigned to five conditions: (1) novel items (N), (2) semantically related target list items (RT), (3) semantically unrelated target list items (URT), (4) semantically related distractor list items (RD), and (5) semantically unrelated distractor list items (URD). Target list and distractor list were counterbalanced in order to control for list positioning effects.

According to our hypothesis, the retrieval of items assigned to the semantically related conditions would cause cognitive interference, thus leading to significantly longer reaction times. Statistical analysis of the behavioral data from the pilot study of the paradigm confirmed this hypothesis and revealed significantly longer reaction times for correct responses in the interference conditions ($\text{mean}_{\text{RT}}: 1,446 \pm 450 \text{ ms}$; $\text{mean}_{\text{RD}}: 1422 \pm 465 \text{ ms}$) compared to the noninterference conditions ($\text{mean}_{\text{URT}}: 882 \pm 123 \text{ ms}$; $\text{mean}_{\text{URD}}: 791 \pm 185 \text{ ms}$; $\text{mean}_{\text{N}}: 674 \pm 146 \text{ ms}$).

Experimental procedure

The analysis of online-recorded behavioral data from two subjects performing the experiment in the scanner showed a significant decrease of reaction times when responding to the RT and RD conditions. Reevaluation of the experimental setup revealed that both subjects—although not aware of the following task—used the time between the end of the learning period and the beginning of the experimental runs for intensive rehearsal of the word lists. Therefore, we decided to introduce a distractor task bridging the delay between completion of the learning period and beginning of the functional scanning. This distractor task consisted of a continuous performance paradigm (one-back visual working memory task) and lasted about 10 min. The symbols “X”, “I,” and “O” were projected to a front-projection screen in random order (stimulus presentation time = 500 ms, ISI = 2,500 ms) and subjects were instructed to respond as quickly as possible with the left-hand index finger as soon as two Xs appeared in sequence. All subjects were informed of the recognition task just before the beginning of the experimental runs. After implementation

of the distractor task, the behavioral data again followed the same pattern as in the pilot study (see Results). A graphic representation of the experimental paradigms and experimental procedure is given in Figure 1.

Functional MRI scanning techniques and data analyses

Imaging was performed with a GE Medical Systems 1.5 Tesla SIGNA neurovascular MR scanner equipped with a fast gradient EPI system and a standard GE quadrature head coil. Visual images were front-projected to participants from an IBM computer; participants viewed the images through a mirror on the head coil. To minimize artifacts arising from head motion, foam cushioning was placed snugly around the side and back of the participants’ head. Participants indicated their responses to the recognition task with their left (nondominant) hand using a magnet-compatible key press.

Conventional structural images that provided detailed anatomic information were first acquired (high-resolution rf-spoiled GRASS sequence, 60 slice sagittal, 2.8 mm thickness), followed by functional images sensitive to blood oxygenation level-dependent contrast (echo planar T2*-weighted gradient echo sequence, TR = 2 s, TE = 30 ms, flip = 90°). During the acquisition of structural images all subjects performed the continuous-performance distractor task. The instruction for the recognition task was given just before the beginning of the functional sessions. Each functional run consisted of 170 sequential whole-brain acquisitions (16 axial slices aligned to the plane intersecting the anterior and posterior commissures, 3.125 mm in-plane resolution, 7 mm thickness, skip 1 mm between slices). The first 10 volumes of each run served as dummies and were discarded from analysis. The presentation of the first stimulus was synchronized with the scanner and started 21 s after the beginning of each run. A run consisted of 80 trials. Trials of each run were composed of 20 items from the target list, 20 items of the distractor list, and 40 novel items presented in pseudorandom order. This arrangement resulted in the acquisition of a total of 800 volumes for the analysis of memory retrieval related data sets.

A detailed description of the procedures for selective averaging and statistical map generation is given elsewhere [Buckner et al., 1998b; Dale and Buckner, 1997]. Briefly, data from individual fMRI runs were first normalized to correct for global between-run signal intensity changes and temporal drift. The normalized data were then selectively averaged in relation to

Figure 1.

Graphic representation of the experimental paradigm and experimental procedure. The experimental paradigm consisted of three tasks: In the learning condition, subjects were instructed to learn a first 20-item word list (target list) and immediately thereafter a second 20-item word list (distractor list) both to 100% criterion. Items were assigned to six semantic categories, two of which were identical in target and distractor list (shadowed). During the set-up period and acquisition of structural images, all subjects had to perform a distractor task in order to prevent active rehearsal of the previously learned word lists. This distractor task consisted of a continuous performance paradigm (one-back task) and lasted about 10 min. The letters “I,” “O,” and “X” were projected in random order and subjects had to respond with a “yes”-button press (left index finger) every time two “X”s appeared in sequence. In the retrieval condition, words from the previously learned target and distractor lists were used together with unique words that were not semantically related to the semantic categories

of the target or distractor lists. Subjects were instructed to respond as quickly as possible with the left-hand index finger in all cases where the presented noun (S) matched an item from the target list. For all other items (distractor list and novel words), subjects had to use the left-hand middle finger for a “no” response. During functional scanning, 400 stimuli consisting of target-list words, distractor-list words, and novel (semantically unrelated) words were projected during five runs separated by a 2-min rest period. Each run consisted of a block of 80 trials with 20 target-list nouns, 20 distractor-list nouns, and 40 novel nouns presented in pseudorandom order. Nouns from the target and distractor list were repeated within every run whereas novel and semantically unrelated nouns were presented only once. During each run 170 sequential whole-brain acquisitions were collected. This design resulted in a total of 400 trials and 800 trial related volumes. To avoid prefrontal activation induced by false recognition, analysis of fMRI data was based on correct responses only.

the beginning of each trial type. After all trials were selectively averaged for each subject, the mean and variance images were transformed into the stereotaxic atlas space [Talairach and Tournoux, 1988] allowing for across-subject averaging. Thereafter, statistical activation maps were constructed based on the differences between trial types using t-statistics. Clusters of five or more voxels exceeding a statistical threshold of $P < .001$ were considered significant foci of activation. These criteria have been found to result in the identification of few false positives in control data sets [Buckner et al., 1998a; Wagner et al., 1998b]. An automated algorithm was used to identify significant peaks of activation; when significant peaks occurred within 10 mm of one another, the most significant peak was retained. Finally, an ROI analysis was performed on an automated procedure reconstructing significant voxels around the detected peak activation. The temporal distribution of the BOLD response was analyzed based on these clusters, with the mean and variance provided by a selective average procedure.

RESULTS

Behavioral data

The median number of trials for word list learning to 100% criterion was three (target list: $mdn = 3$, range: 2–5; distractor list: $mdn = 3$, range 2–4). Both qualitative and quantitative analysis of online-recorded behavioral data confirmed our hypothesis of cognitive interference resulting from the retrieval of semantically related item sets. Accuracy ($P_{hits} - P_{false\ alarms}$) significantly differed across the conditions (Friedman two-way ANOVA: $\chi^2_{[2]} = 15.9$, $P = .0003$). It was almost perfect in the novel item condition (N: accuracy = 0.99) followed by the noninterference conditions (NIC; consisting of semantically unrelated targets [URT] and semantically unrelated distractors [URD]: accuracy = 0.95) and the interference conditions (IC; consisting of semantically related targets [URT] and semantically related distractors [RD]: accuracy = 0.66). This pattern of performance was consis-

tently found in all subjects. A repeated measure ANOVA revealed highly significant effects of retrieval condition ($F_{[2,16]} = 39.8, P < .0001$) and run ($F_{[4,32]} = 49.0, P < .0001$) and a significant interaction between condition and run ($F_{[8,64]} = 3.3, P = .003$). A detailed analysis of error rates demonstrated that the poor IC performance could not be attributed to the RT or the RD condition. Error rates in both conditions were nearly the same (RT: 16.7% errors; RD: 17.1% errors; $t_{[8]} = -.058; P = .955$). Furthermore, the NIC performance did not differ significantly with respect to the target or distractor list items (URT: 1.8% errors; URD: 3.1% errors; $t_{[8]} = -.918; P = .386$). These data indicate that interference was evoked by semantically related items and not by a temporal position effect of item lists (i.e., source interference). Figure 2a shows that the reaction time of correct responses in the interference conditions were significantly longer when compared to the noninterference ($t_{[8]} = 5.0, P = .001$) that were, in turn, significantly longer than the responses to novel stimuli ($t_{[8]} = 7.7; P < .0001$). This pattern of reaction times was the same in each of the nine subjects. The analysis of memory performance and response latencies clearly indicate considerable differences in retrieval success and retrieval effort across the retrieval conditions with the highest task load in the interference conditions. Figure 2b additionally shows that the reaction time significantly decreased across the five runs. This slope of reaction time was highly significant for all retrieval conditions (repeated measure ANOVA: IC: $F_{[4,32]} = 24.8, P = .001$; NIC: $F_{[4,32]} = 61.3, P < .0001$; N: $F_{[4,32]} = 24.7, P = .001$). Memory performance, however, did not improve across the five runs as indicated by stable error rates (Friedman two-way ANOVA: IC: $\chi^2_{[4]} = 3.25, P = .516$; NIC: $\chi^2_{[4]} = 3.27, P = .514$; N: $\chi^2_{[4]} = 3.50, P = .478$).

Functional MRI data

As the main purpose of the present study was the analysis of activation patterns associated with the control of semantic interference in episodic memory retrieval, we primarily focused on the direct contrast of the interference against the noninterference condition. The subcomponents of these tasks did not differ with the exception of a higher retrieval effort and lower retrieval success in the interference condition (as indicated by significantly longer response latencies and a significantly higher error rate). In order to avoid prefrontal activation induced by false recognition [Schacter et al., 1996b], analysis of fMRI data was based on correct responses only. Contrasting the interference condition against the noninterference con-

Figure 2.

Behavioral data analysis: (a) both the target and distractor interference conditions (IC: semantically related targets (RT) and semantically related distractors (RD)) resulted in significantly longer mean reaction times compared to the noninterference condition (NIC: semantically unrelated targets (URT) and semantically unrelated distractors (URD)) and the novel stimulus condition (N). (b) reaction times (lines; left axis) continuously decreased from run 1 to run 5; the error rate (bars, right axis) was significantly higher in the interference condition and remained stable across all five runs. Error bars indicate standard error of mean.

dition revealed three suprathreshold foci of activation in the PFC and the anterior cingulate/medial frontal cortex. The right-lateralized pattern comprised the activation of an anterior medial frontal region encompassing the dorsal anterior cingulate cortex (BA 32) and the adjacent medial frontal cortex and a ventral prefrontal region encompassing the frontal opercular area of the inferior frontal gyrus (BA 45). The left-lateralized activation focus consisted of a dorsolateral PFC area with the highest contrast in the middle frontal gyrus (comprising BA 6/9). The locations of peak activation are shown in Table I.

In order to analyze further the activation pattern of semantic interference in episodic memory retrieval we included the information derived from the processing

TABLE I. Activation maxima^a

Region of activation	BA	Left/right	No. of voxels	Talairach coordinates			P
				x	y	z	
Medial frontal	6	R	24	3	13	53	8.4×10^{-6}
Frontal opercular	45	R	18	34	25	6	2.2×10^{-5}
Frontal opercular	45	R	18	34	19	9	4.3×10^{-5}
Anterior cingulate	32	R	25	6	22	43	6.3×10^{-5}
Precentral/middle frontal	6/9	L	24	-35	0	40	1.9×10^{-4}

^a Analysis is based on the interference vs. noninterference direct contrast. Peaks are shown that are more significant than $P < .001$. Peaks must be within a cluster of five voxels and must be separated by 8 mm or else only the largest is kept.

of novel items which was neglected in the previous analysis. Recent fMRI studies on the processing of novel and familiar words demonstrated an activation pattern including the PFC and the anterior cingulate when subjects correctly identified familiar (learned) items [e.g., Saykin et al., 1999]. In order to analyze whether the activated areas demonstrated in Figure 3 were selectively engaged during the control of semantic interference, we analyzed the temporal profile of the BOLD response with respect to interference control and recognition of old and new items. Figure 4 shows the percent signal changes in trial averaged time series in the areas demonstrating the mean effect at the interference versus noninterference contrast (see Table I). The contrasts are demonstrated between the interference versus noninterference condition (solid line) and between the old (noninterference) versus novel condition (dotted line). In all ROIs, the interference versus noninterference condition showed an increase in signal change with a time shift reflecting the low pass filtering properties of the hemodynamic response. In contrast, the comparison between old (semantically unrelated) and novel words only resulted in an increase of signal change in the dorsal anterior cingulate region, whereas both dorsolateral PFC and frontal opercular area showed no significant effect.

DISCUSSION

In the present study we could demonstrate PFC areas that were selectively engaged when the memory retrieval task required the monitoring of competing information-processing streams. The cognitive sub-components of the recognition task in the interference and noninterference conditions did not differ, with the only exception of an active response inhibition process when the subjects correctly responded to the semantically related items from the target and distractor word lists. The latter condition was obviously associated with a higher demand of monitoring and evalu-

ation of the stimuli with respect to the mnemonic representation of the whole set of learned words. This increase of monitoring effort was reflected by significantly longer reaction times and a significantly lower accuracy during the interference condition. Contrasting the interference against the noninterference condition revealed an activation pattern that comprised a right medial frontal and dorsal anterior cingulate region, a right frontal opercular region, and a left dorsolateral PFC area. Trial type averaged time series of the BOLD signal illustrated that an increase of signal change in the ventrolateral and dorsolateral frontal regions was only observed during the interference versus noninterference contrast, whereas a comparison between the old and new item condition failed to show significant signal changes in these areas. Collectively, these findings corroborate the prominent executive role of the PFC in episodic memory retrieval. Moreover, the present data illustrate that monitoring and control of interference are specific components of the PFC contribution to human memory processing and specify recent findings with respect to the functional representation of task-monitoring demands.

The dorsal subregion of the anterior cingulate cortex (also referred to as anterior cingulate cognitive division [Bush et al., 1998]) has been reported to be involved in episodic memory and working memory conditions. Retrieval-associated activation of the anterior cingulate is a common finding in a variety of word recognition paradigms [Saykin et al., 1999; Wagner et al., 1998a; Henson et al., 1999a]. In a recent study, Petit and colleagues [1998] found a sustained activity during working-memory delays in the medial wall. This activation pattern comprised the pre-SMA and the dorsal anterior cingulate and was found during both spatial and face working memory delays. These areas were clearly separable from simple motor-/oculomotor-related activity that resulted in a more posterior activation of the SMA proper, the supplementary eye field, and the cingulate motor area. A predominant

Figure 3.

Average activation map. Axial and coronal slices showing the contrast between the interference and noninterference retrieval condition averaged across all subjects. The contrasts are based on correct responses only.

anterior cingulate activation pattern was also reported in several studies of interference control based on Stroop (word-color) tasks [Carter et al., 1995, 2000; Peterson et al., 1999] or Stroop-like (counting) tasks [Bush et al., 1998, 1999]. In the present study, we found a medial frontal / anterior cingulate activation in both the contrast between semantically interfering

and noninterfering items and the contrast between old and novel items. This finding suggests that the role of a medial wall activation in episodic memory retrieval might reflect the task-inherent working memory demands [Petit et al., 1998], including strategic processes such as the online detection of conflicting information [Cohen et al., 2000] and the subsequent up- or down-

Figure 4.

Trial-averaged time series. The graphs demonstrate the percentage signal changes of subject-averaged mean data from the voxels showing the mean effect at the interference vs. noninterference direct contrast.

regulation of the allocation of attention resources [Posner and Dehaene, 1994]. Therefore, a stronger medial wall engagement is observed in tasks that require the control of competing information streams and active response inhibition. This hypothesis is also substantiated by a most recent fMRI study on the anterior cingulate contribution on the monitoring of conflicting responses [Barch et al., 2000]. The authors could demonstrate a stronger anterior cingulate engagement in task conditions evoking competition of alternative responses in a verb generation paradigm.

Frontal opercular and adjacent anterior insular and posterior inferior frontal cortex activation were also reported in episodic retrieval studies [Wagner et al., 1998a; Buckner et al., 1996]. It was not considered specific for episodic memory retrieval as similar activation patterns were also found in a variety of other conditions, including auditory and phonological pro-

cessing [Fiez et al., 1995], memory formation [Wagner et al., 1998b], and working memory performance [D'Esposito et al., 1999b]. Ventrolateral PFC activation is a frequent finding in tasks that require the selection and inhibition of responses in the selective attention or working memory domain. Konishi and colleagues [1998a] demonstrated bilateral shift-related activity in the posterior parts of the inferior frontal sulci when subjects performed a computerized version of the Wisconsin Card Sorting Test. In a task-switching paradigm similarly provoking a shift of cognitive sets, Dove and colleagues [2000] observed a bilateral anterior insula activation in the task-switch condition. Response inhibition elicited by a go/no-go task [Konishi et al., 1998b] showed a no-go dominant brain activity in the posterior part of the right inferior frontal sulcus. This activation pattern was consistently right-lateralized irrespectively of whether the left or right hand was used for button press and partially overlapped the activation area found in the Wisconsin Card Sorting Task [Konishi et al., 1998a, 1999]. A left ventrolateral PFC activation encompassing anterior insular, frontal opercular, and posterior inferior frontal cortex regions was found by D'Esposito et al. [1999a] with a n-back working-memory paradigm provoking a proactive interference effect. Based on this finding, the authors argued that ventrolateral but not dorsolateral PFC subserves interference control or response inhibition. The results of our present study of semantic interference control in episodic memory retrieval are in line with the findings cited above. The ventrolateral PFC was selectively engaged only in conditions in which subjects had to inhibit an inherent response tendency provoked by the semantically interfering items from the target and distractor word lists. The present data also corroborate previous studies that demonstrated that PFC activation patterns in episodic memory retrieval are dependent on the retrieval context [Wagner et al., 1998a; Henson et al., 1999a]. Henson and colleagues [1999a] hypothesized that a ventral region of the right PFC is sensitive to the retrieval mode, whereas a dorsal region of the PFC is associated with the monitoring demand of episodic memory retrieval.

We cannot offer an explanation for the left-lateralization of the dorsolateral PFC activation and the right-lateralization of the ventrolateral PFC activation that we suppose subserves the monitoring/evaluation and the inhibition or release component of the interference control process. At present we can only speculate that the laterality of activation of the dorsolateral area might be attributed to the semantic processing demands of our recognition task, thus possibly reflect-

ing a material-specific lateralization [Kelley et al., 1998; Buckner et al., 1999].

CONCLUSIONS

In the present study we showed that the control of interfering information in episodic memory retrieval resulted in an anterior cingulate-prefrontal activation pattern. This finding helps to additionally clarify and to substantiate the role of the PFC in episodic recognition memory. The present findings indicate that the control of semantic interference in episodic memory retrieval selectively engages specific PFC areas. The data give support to the idea that the PFC activation as part of the executive control of episodic memory processing includes both ventral and dorsal PFC areas similar to those found in working memory tasks.

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