

Frontal Brain Activity during Episodic and Semantic Retrieval: Insights from Event-Related Potentials

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Abstract

■ Previous neuropsychological and neuroimaging results have implicated the prefrontal cortex in memory retrieval, although its precise role is unclear. In the present study, we examined patterns of brain electrical activity during retrieval of episodic and semantic memories. In the episodic retrieval task, participants retrieved autobiographical memories in response to event cues. In the semantic retrieval task, participants generated exemplars in response to category cues. Novel sounds presented intermittently during memory retrieval elicited a series of brain potentials including one identifiable as the P3a potential. Based on prior research linking P3a with novelty

detection and with the frontal lobes, we predicted that P3a would be reduced to the extent that novelty detection and memory retrieval interfere with each other. Results during episodic and semantic retrieval tasks were compared to results during a task in which subjects attended to the auditory stimuli. P3a amplitudes were reduced during episodic retrieval, particularly at right lateral frontal scalp locations. A similar but less lateralized pattern of frontal P3a reduction was observed during semantic retrieval. These findings support the notion that the right prefrontal cortex is engaged in the service of memory retrieval, particularly for episodic memories. ■

INTRODUCTION

The memory functions of the prefrontal cortex have historically been a topic of considerable debate. Findings from human and nonhuman primates with prefrontal lesions have been used to support the idea that prefrontal areas play a key role in several functions, including selective attention (Knight & Grabowecky, 1995; Luria, 1973a, 1973b; Pribram, 1973; Shallice, 1982) and working memory (Fuster, 1989; Goldman-Rakic, 1987). However, prefrontal memory functions may go beyond working memory. In particular, recent neuropsychological and neuroimaging results suggest that the prefrontal cortex may also play a role in long-term memory, which includes *semantic memory* (memory for facts or general knowledge) and *episodic memory* (memory for specific events; Tulving, 1972). Here we report on pertinent electrophysiological results and their relationship to evidence from neuropsychology and neuroimaging.

Neuropsychology

Frontal lesions generally do not produce a classic amnesic syndrome but instead produce subtle episodic memory deficits in some circumstances. On verbal free recall tests thought to tax episodic memory, moderate deficits have been reported in patients with prefrontal damage (Gershberg & Shimamura, 1995; Hirst & Volpe, 1988;

Incisa della Rochetta & Milner, 1993; Jetter, Poser, Freeman, & Markowitch, 1986; Stuss et al., 1994). However, these deficits were ameliorated with instructions to use particular encoding and retrieval strategies (Gershberg & Shimamura, 1995; Hirst & Volpe, 1988; Incisa della Rochetta & Milner, 1993). Frontal patients also showed significant deficits on tasks assessing memory for source (Janowsky, Shimamura, & Squire, 1989b) and temporal order (Butters, Kaszniak, Glisky, Eslinger, & Schacter, 1994; Mangels, 1997; McAndrews & Milner, 1991; Milner, Corsi, & Leonard, 1991; Shimamura, Janowsky, & Squire, 1990), but again, these deficits were not found when enriched encoding tasks were given (Butters et al., 1994; McAndrews & Milner, 1991; Mangels, 1997). Patients with frontal lesions performed normally on paired associate learning (Janowsky, Shimamura, Kritchevsky, & Squire, 1989a; Shimamura, Jurica, Mangels, Gershberg, & Knight, 1995), word-stem cued recall (Swick & Knight, 1996), and story learning tasks (Janowsky et al., 1989a). On tests of recognition memory, patients with prefrontal damage have shown mild impairments (Wheeler, Stuss, & Tulving, 1995). In summary, patients with frontal lesions perform at normal levels on episodic memory tests with highly structured materials and external retrieval cues but are impaired on tests with relatively unstructured material and minimal retrieval cues.

Therefore, the key contribution of the prefrontal cortex may be in the use of strategies at encoding and at

retrieval (Mayes, 1988; Milner, Petrides, & Smith, 1985; Moscovitch, 1989). Additional support for this view comes from studies of a patient with right frontal damage, B.G., who demonstrated extremely high rates of false alarms on recognition memory tests (Schacter, Curran, Galluccio, Milberg, & Bates, 1996; Curran, Schacter, Norman, & Galluccio, 1997). These researchers concluded that false recognition in B.G. was due to his overreliance on the general similarity between test items and items from the study episode.

If the prefrontal cortex is critical for strategic retrieval of information from memory, patients with prefrontal lesions should also be impaired on tasks requiring effortful retrieval of semantic information, not just episodic information. Indeed, patients with left frontal lesions have shown deficits on letter fluency tasks in which patients attempt to generate different words beginning with a given letter (Benton, 1968; Butler, Rorsman, Hill, & Tuma, 1993; Gershberg & Shimamura, 1995; Janowsky et al., 1989a; Milner, 1964). Patients with left frontal lesions have also shown impairments on a test that required patients to make living/nonliving judgments (Swick & Knight, 1996).

Neuroimaging

Recent neuroimaging results from normal participants also support the notion that prefrontal processing is critical for strategic search and retrieval operations (Buckner & Tulving, 1996; Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Summarizing findings from 31 positron emission tomography (PET) studies of episodic retrieval, Nyberg et al. (1996) noted that 29 reported significant frontal activation. Furthermore, in 26 of these studies, these prefrontal blood flow increases were larger in the right hemisphere. Nyberg and colleagues also reviewed 16 studies involving semantic retrieval tasks; 13 of these reported significant prefrontal activations, all in the left hemisphere. These laterality patterns were first noted in the Hemispheric Encoding Retrieval Asymmetry (HERA) model of episodic memory put forward by Tulving et al. (1994). According to this model:

The left prefrontal cortex is differentially more involved in retrieval of information from semantic memory, and in simultaneously encoding novel aspects of the retrieved information into episodic memory, than is the right prefrontal cortex. The right prefrontal cortex, on the other hand, is differentially more involved in episodic memory retrieval than is the left prefrontal cortex. (Nyberg et al., 1996, p. 138)

This emphasis on the laterality of PET activations is notable because it represents neurophysiological support for Tulving's (1972) distinction between semantic and episodic memory. In addition, determining the

unique memory functions of left and right frontal regions should be useful for characterizing the distinctive neurocognitive architecture of episodic and semantic memory.

Brain Potentials

An alternative method of monitoring brain activity during memory retrieval is to record electrophysiological responses time-locked to stimulus events. Event-related potentials (ERPs) provide measures of neural activity that may be more direct than neuroimaging based on subsequent hemodynamics. Although current ERP methods do not provide precise neuroanatomical localization, the temporal resolution of ERPs allows critical events to be monitored over the course of milliseconds—some such events may be too brief to elicit a reliable hemodynamic response. ERPs can also be measured with or without subtraction from a reference task. Thus, the ERP method provides a source of evidence to complement neuroimaging in the evaluation of neurobiological models of memory retrieval. Although there have been numerous studies of ERPs during episodic memory tasks (for reviews see Johnson, 1995; Paller, 1993; Rugg, 1995), patterns of brain activity during episodic and semantic retrieval have seldom been directly compared.

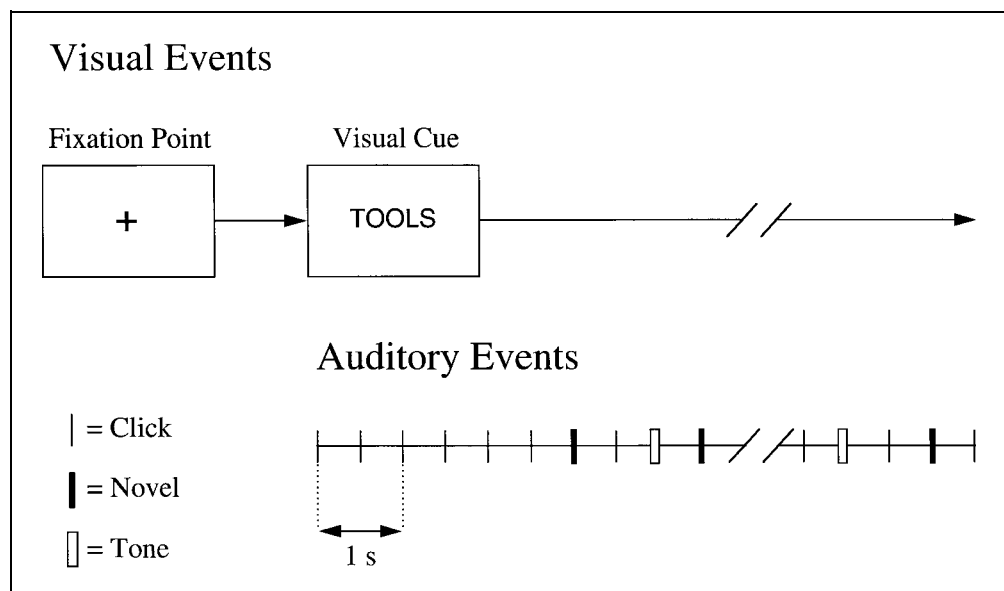
The purpose of the present study was to make just such a comparison, using a measure of regional activation derived from prior work on *P3a*, an ERP component that typically reaches maximum amplitude 200 to 300 msec after a stimulus that is unpredictable, novel, and task-irrelevant (Friedman, Kazmerski, & Cycowicz, 1998; Knight, 1984, 1997; Squires, Squires, & Hillyard, 1975; Yamaguchi & Knight, 1991). In contrast, *P3b* is an ERP component that peaks later and is enhanced to the extent that stimuli are task-relevant (Squires et al., 1975). These two components are additionally differentiated by their scalp topographies; *P3a* has a more anterior distribution across the scalp than does *P3b*. Moreover, neuropsychological findings indicate that the prefrontal cortex is critical in the generation of *P3a*. In patients with unilateral prefrontal lesions, *P3a* amplitude reductions have been observed on the side of the lesion, whereas *P3b* amplitude is typically unaffected (Knight, 1984, 1997; Yamaguchi & Knight, 1991). To account for these findings, Knight (1997) proposed that the prefrontal cortex is part of a distributed cortical network for orienting to novel stimuli.

Based on this evidence regarding *P3a*, we made the following speculations. If novel stimuli are presented while another task engages prefrontal retrieval processing, fewer resources would be available for novelty detection, and *P3a* potentials would be reduced in amplitude. In this way, we reasoned that topographically specific reductions in *P3a* amplitude could provide measures of regional brain activity during memory retrieval. Based on this hypothesized competition for the

allocation of processing resources to memory retrieval and novelty detection, we used P3a amplitude to monitor frontal brain activity during semantic and episodic retrieval.

Participants performed episodic and semantic retrieval tasks while a series of clicks, novel sounds, and tones were presented (see Figure 1). Episodic retrieval was engaged by using the cue word paradigm to elicit retrieval of autobiographical memories (Crovit & Schiffman, 1974; Galton, 1883). We chose this task because prior studies have associated frontal dysfunction with deficits in autobiographical memory retrieval (Baddeley & Wilson, 1987; Della Salla, Laiacona, Spinnler, & Trivelli, 1993; Moscovitch, 1989; Stuss, Alexander, Lieberman, & Levine, 1978). Semantic retrieval was engaged by requiring participants to generate exemplars in response to a category name. We chose this task because prior studies have associated frontal dysfunction with deficits in verbal fluency (Benton, 1968; Butler et al., 1993; Janowsky et al., 1989a; Milner, 1964). We also included a baseline task in which participants were asked to attend to the auditory stimuli and mentally count the tones. All three tasks were performed silently. At the end of each trial, the participant was asked to describe the retrieved memory (episodic task), to name exemplars generated (semantic task), or to state the number of targets counted (tone-counting task). Our key results involved frontal ERPs to novel sounds during memory retrieval and tone counting. Based on the reasoning described above, we predicted that frontal P3a amplitudes would be reduced on the right during episodic memory retrieval and on the left during semantic retrieval.

Figure 1. Schematic depiction of a single trial. Each trial included a different visual cue and a sequence of auditory stimuli comprised of 20 clicks, 5 novel sounds, and 1-5 pure tones in a pseudorandomized order (see Methods for further details).



RESULTS

Behavioral Measures

In the tone-counting task, count accuracy was nearly perfect, averaging 97% correct ($SD = 0.03\%$). In the episodic retrieval task, posttrial ratings of vividness and temporal context were obtained to verify that participants retrieved a specific autobiographical memory. The mean vividness rating across participants was 3.07 ($SD = 0.340$) and the mean temporal detail rating was 3.26 ($SD = 0.324$), both out of a possible 4. These high ratings from the episodic retrieval condition suggest that participants were actively engaged in recollecting autobiographical episodes during ERP recording. Likewise, in the semantic task, participants were able to generate at least four exemplars on 97.5% of the trials ($SD = 0.043\%$).

Electrophysiological Measures

Figure 2 shows midline ERPs to novel sounds, tones, and clicks for each task. In all three tasks, ERPs to novel sounds included a positive deflection with a peak latency of approximately 240 msec and maximal amplitude at the central midline scalp location. Based on functional and waveform characteristics, this deflection can be identified as a P3a component. Tones elicited a later positive deflection but only in the tone-counting condition. This deflection reached a peak amplitude at approximately 400 msec at posterior scalp locations and can be identified as the P3b component. An initial quantification of P3a and P3b in the tone-counting task was done by measuring mean amplitudes from 200 to 400 msec for novel sounds and 300 to 500 msec for tones, respectively. Maps showing the distribution of these potentials across the scalp (Figure 3) highlight topographic differences between the two components.

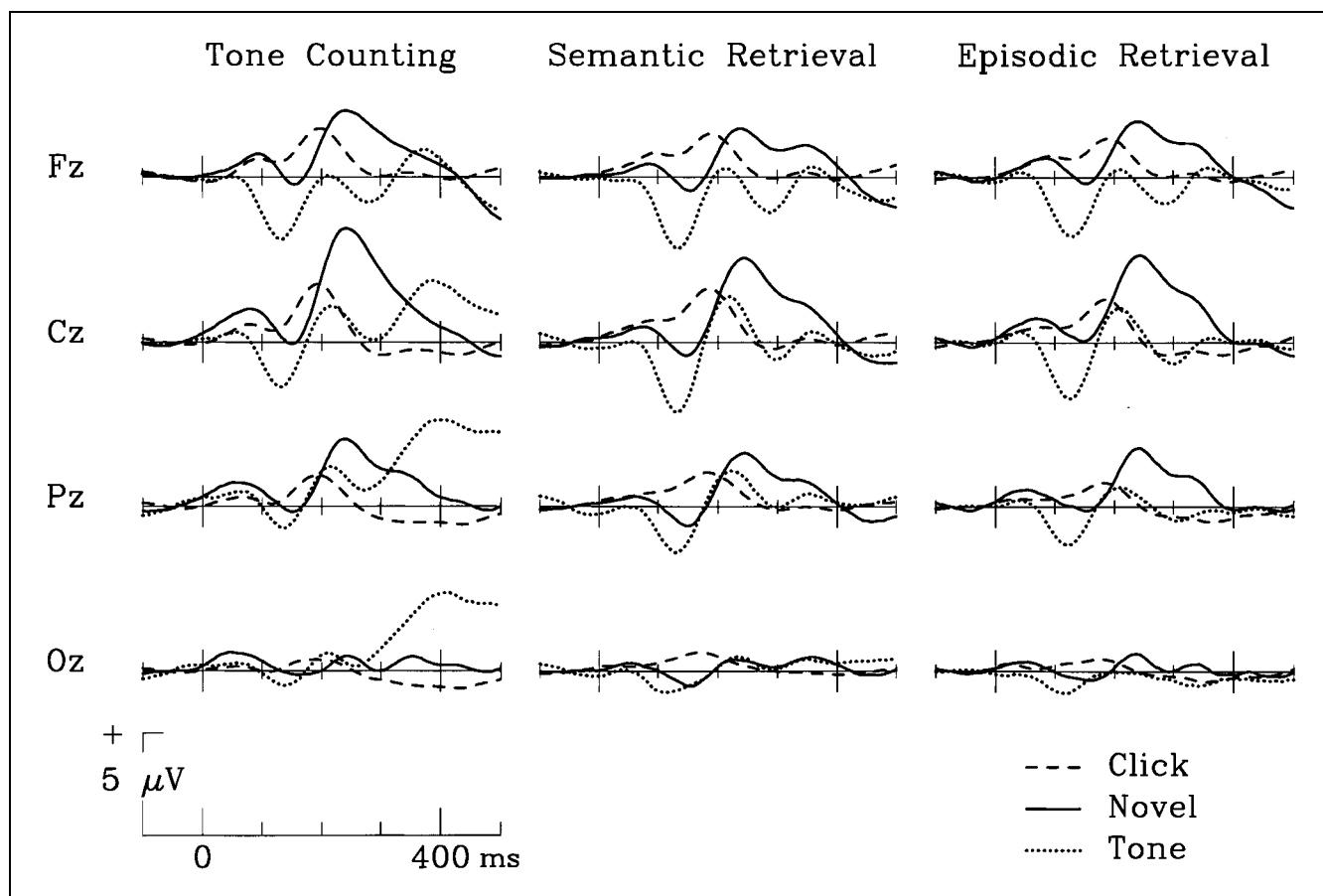


Figure 2. ERPs to the three types of auditory stimuli presented during each task. Recordings are shown from four midline scalp locations: frontal, central, parietal, and occipital.

Figure 4 shows left and right frontal ERPs to novel sounds for each task. To test whether P3a was influenced by task, we performed separate analyses of variance (ANOVAs) on P3a amplitudes to novel sounds from each pair of lateral sites, using mean amplitude measurements from 200 to 400 msec. At lateral frontal sites (F7 and F8), there was a nonsignificant main effect for Task ($F(2,$

$22) = 1.72; p = 0.20$) and a marginal main effect for Hemisphere ($F(1, 11) = 4.51; p = 0.057$). More importantly, a significant Task \times Hemisphere interaction ($F(2, 22) = 3.58; p = 0.045$) indicated that differences between left and right frontal ERPs varied across the three tasks. Marginal interactions were also observed at anterior frontal sites (Fp1/Fp2: $F(2, 22) = 3.21; p = 0.06$) and

Figure 3. Topographic maps of P3a and P3b amplitudes during the tone-counting task, as computed by a surface spline interpolation. Each circle represents an electrode location on the scalp, as viewed from above. P3a was measured in ERPs to novel sounds as the mean amplitude from 200 to 400 msec. P3b was measured in ERPs to target tones as the mean amplitude from 300 to 500 msec.

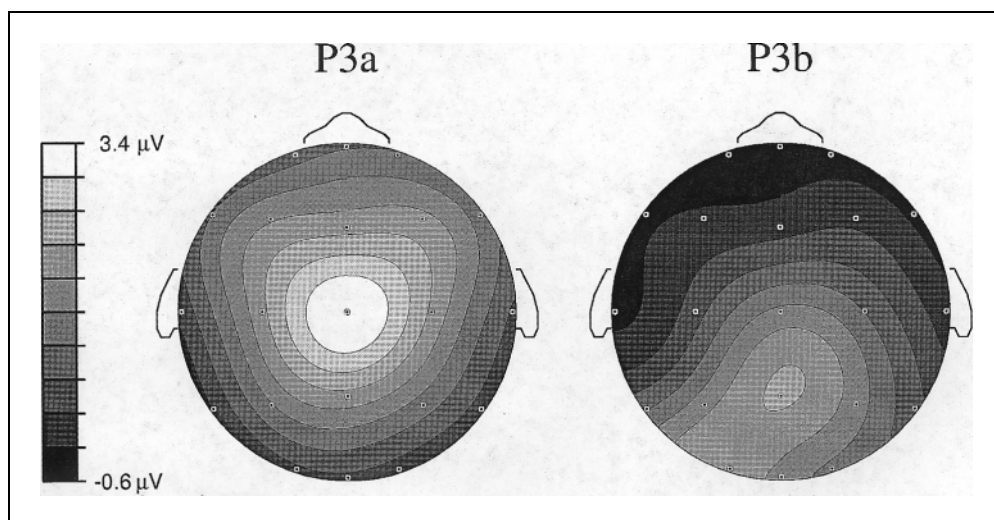
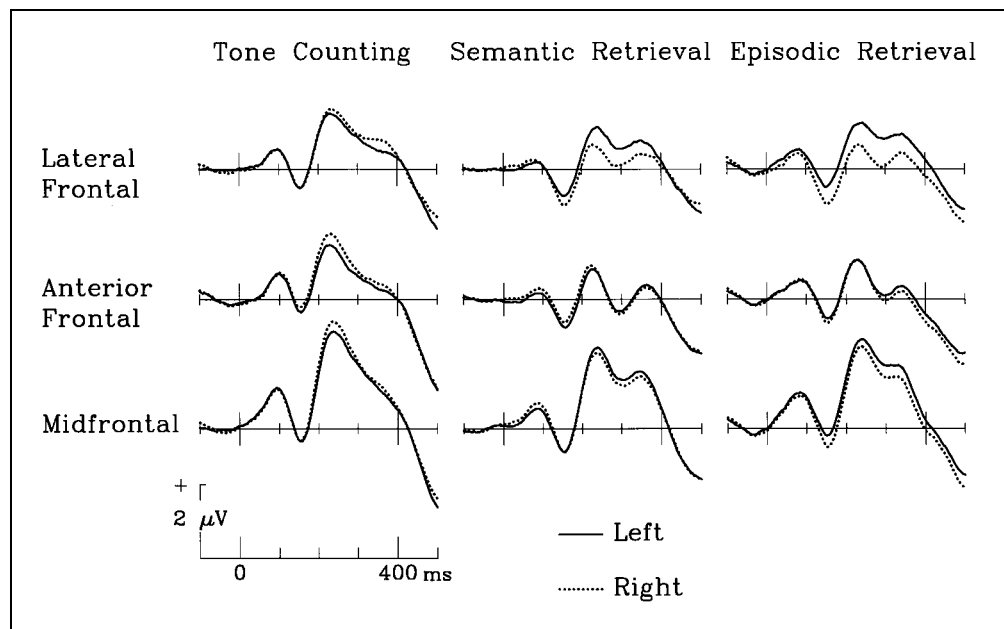


Figure 4. Left and right frontal ERPs to novel sounds presented during each task. Recordings are shown from lateral frontal (F7/F8), anterior frontal (Fp1/Fp2), and midfrontal (F3/F4) scalp locations.



midfrontal sites (F3/F4: $F(2, 22) = 3.34$; $p = 0.054$) with no significant main effects in any of these analyses (all $F(1, 11)s < 1.30$). No significant main effects or interactions were observed in the analyses on central (C3/C4), temporal (T3/T4, T5/T6) or occipital (O1/O2) electrode pairs (all $Fs < 1.30$).

P3a amplitude measurements at lateral frontal sites are shown for each condition in Figure 5A. To follow up the significant Task \times Hemisphere interaction and directly test our hypothesis that P3a would be reduced during memory retrieval, we conducted t tests comparing P3a at lateral frontal scalp locations during memory retrieval versus tone counting (i.e., taking tone counting as the baseline). Results showed that right frontal P3a was smaller during episodic retrieval than during tone counting ($t(11) = 2.19$; $p = 0.05$), whereas left frontal P3a differences were nonsignificant ($t(11) < 1$). Similarly, right frontal P3a was smaller during semantic retrieval than during tone counting ($t(11) = 2.95$; $p = 0.013$), whereas left frontal P3a differences were nonsignificant ($t(11) < 1$).

As expected, the memory retrieval tasks appeared to interfere with novelty detection processes. However, these results may have been influenced by the fact that each novel sound was repeated four times over the course of the experiment. Prior research has demonstrated that ERP responses to novel stimuli decline with repetition (Courschesne, Hillyard, & Galambos, 1975; Friedman et al., 1998; Knight, 1984). Therefore, we also analyzed P3a amplitudes confined to data from the first block (when each sound was heard for the first time). Measurements from lateral frontal sites during the first block are shown in Figure 5B. A repeated measures ANOVA with Task and Hemisphere as independent variables revealed a significant Task \times Hemisphere interac-

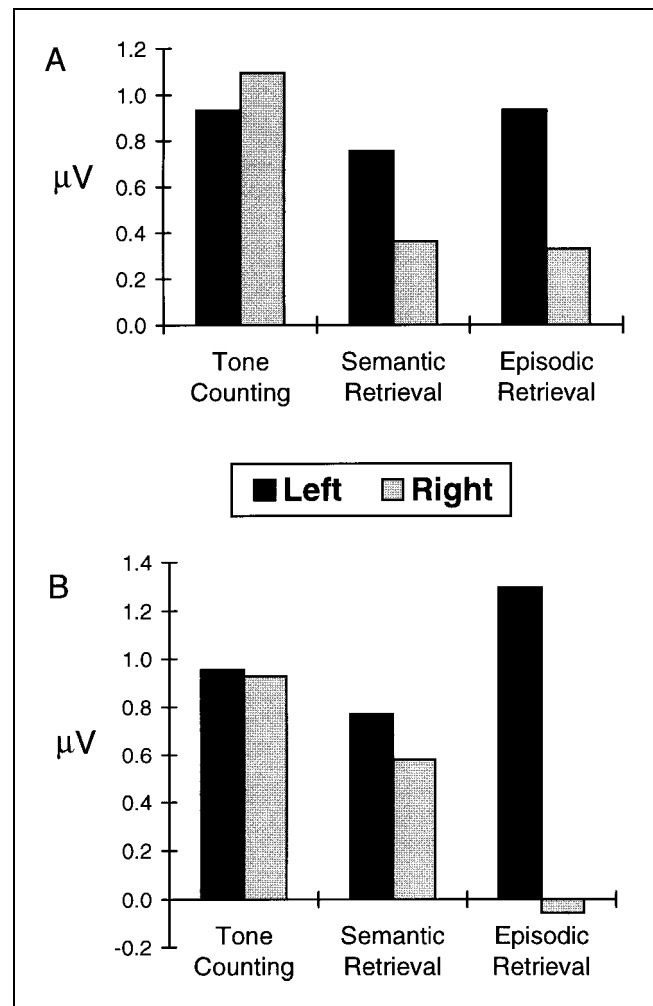


Figure 5. Frontal P3a amplitude measurements in the three task conditions for all four blocks (A) and from the first block only (B). ERPs were measured from lateral frontal scalp locations (F7/F8) from 200 to 400 msec.

tion ($F(2, 22) = 3.34; p = 0.049$). Furthermore, the first-block right frontal P3a was smaller during episodic retrieval than during tone counting ($t(11) = 2.48; p = 0.031$), whereas left frontal P3a differences were nonsignificant ($t(11) < 1$). Differences in P3a between semantic retrieval and tone counting were nonsignificant for both left and right lateral frontal sites ($ts < 1$).

To specifically assess hemispheric asymmetries in frontal P3a, we conducted t tests comparing left and right P3a amplitudes within each task. Lateral frontal P3a amplitudes were found to be asymmetric (right smaller than left) during episodic retrieval ($t(11) = 3.53; p = 0.005$). A parallel trend for asymmetric P3a amplitudes was observed at midfrontal sites ($t(11) = 2.15; p = 0.055$), whereas the left-right difference was nonsignificant at anterior frontal sites ($t(11) < 1$). During semantic retrieval, P3a asymmetries were nonsignificant for lateral frontal, midfrontal, and anterior frontal sites ($t(11) = 1.63; p = 0.131; t(11) < 1$ and $t(11) < 1$, respectively). Likewise, asymmetries during tone counting were nonsignificant between lateral frontal ($t(11) < 1$) and midfrontal sites ($t(11) < 1.15$). At anterior frontal sites, however, P3a amplitudes were smaller on the left than on the right ($t(11) = 2.42; p = 0.034$). We also evaluated P3a asymmetries at lateral frontal sites during the first block when the sounds were most novel. The first-block P3a was significantly smaller at right versus left lateral frontal sites during episodic retrieval ($t(11) = 4.54; p = 0.001$) but symmetrical during semantic retrieval and tone-counting (both $ts < 1$).

Figure 6 shows ERPs to visual cues for each task. Differences in brain activity between retrieval tasks and tone counting emerged 300 to 400 msec after cue onset. At occipital sites, part of this difference may reflect visual imagery invoked during episodic and semantic retrieval, as in a previous experiment in which visual imagery was engaged following auditory word presentations (Gonçalves & Paller, in press). ERP differences of opposite polarity were apparent at frontal and central sites. Differences between episodic and semantic retrieval tasks were relatively small. At occipital sites, for example, ERPs were more positive during the semantic task compared to the episodic task from 600 to 900 msec, but corresponding mean amplitude differences were nonsignificant ($F(1, 11) = 3.71; p = 0.08$).

DISCUSSION

By using a novel method for obtaining ERP measures of regional brain activity, we compared patterns of frontal activation while participants retrieved episodic and semantic memories. We reasoned that if novelty detection and memory retrieval draw upon shared processing resources mediated by the prefrontal cortex, P3a amplitudes would be reduced over frontal regions during memory retrieval. Furthermore, neuropsychological and

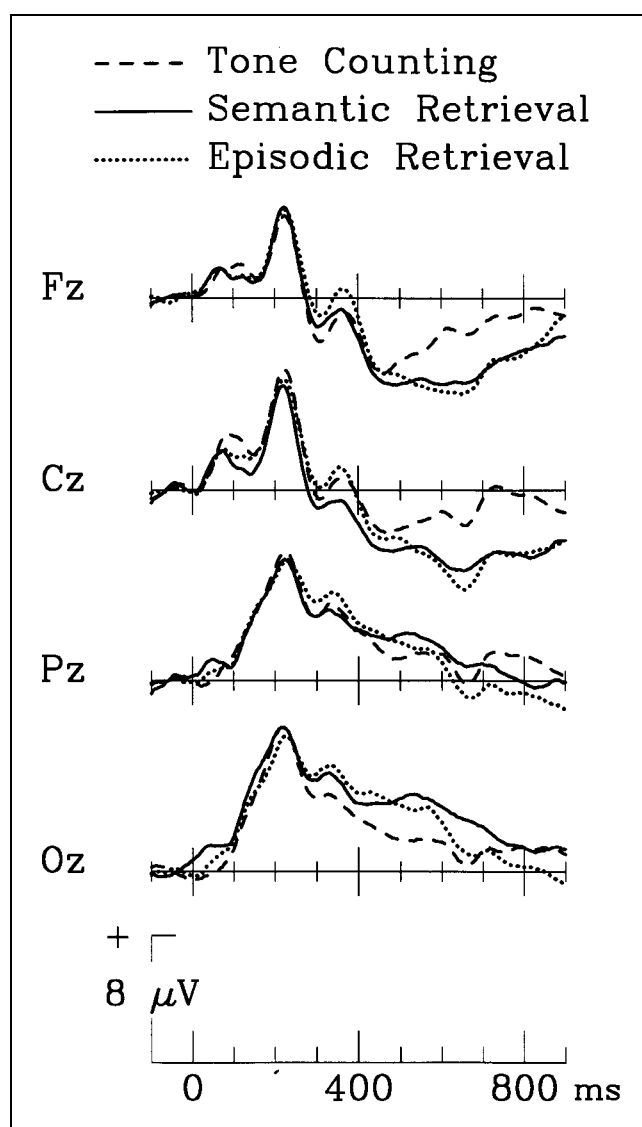


Figure 6. ERPs to visual cues presented during each task. Recordings are shown from four midline scalp locations: frontal, central, parietal, and occipital.

neuroimaging evidence suggested that retrieval of episodic memories would be associated with right frontal activation. Our results showed that during episodic retrieval, P3a was reduced at right frontal sites but not left frontal sites. Although these results cannot be used to precisely locate the sources of differential activity in the brain, they do suggest that right frontal regions were particularly engaged by the episodic retrieval task. This P3a reduction was numerically larger when data from the first block were considered separately (i.e., the first time each novel sound was heard), strengthening the conclusion that episodic retrieval interfered with novelty detection. Unexpectedly, right frontal P3a was also reduced during semantic retrieval. We will consider the implications of the episodic and semantic retrieval effects in turn.

Episodic Retrieval

Our electrophysiological results suggest that right frontal brain regions were active when autobiographical memories were retrieved. Neuroimaging results have similarly been used to support the idea that right frontal regions contribute to episodic retrieval (Buckner, 1996; Buckner & Tulving, 1996; Dalla Barba, Parlato, Jobert, Samson, & Pappata, 1998; Nyberg et al., 1996; Tulving et al., 1994). However, most prior neuroimaging studies used verbal learning paradigms to engage episodic retrieval, whereas participants in the present experiment retrieved autobiographical memories. Apparently, the role played by the right frontal cortex is relevant for both recently acquired verbal material and specific personal episodic memories. This conclusion is in accord with neuropsychological reports of autobiographical memory deficits in patients with right, left, or bilateral prefrontal lesions (Baddeley & Wilson, 1987; Della Salla et al., 1993; Moscovitch, 1989; Stuss et al., 1978). A nontomographic cerebral blood flow study also showed that recollecting personally experienced events was associated with increased blood flow to anterior brain regions (Tulving, 1989).

Right frontal activation was also found using a related type of autobiographical retrieval paradigm (Fink et al., 1996). After an autobiographical interview, participants were scanned while they listened to sentences from their own autobiographies and from those of other participants, with instructions to mentally reenact the episodes from their own lives and to imagine performing the actions described in the sentences of others. PET subtractions (personal sentences minus rest and personal sentences minus sentences from others) revealed several areas of activation in the right hemisphere, including frontal, temporal, and posterior cingulate regions.

If right prefrontal regions are closely involved in the retrieval of autobiographical information, what is their precise function in these tasks? Several answers to this question have been proposed, including execution of strategic search processes (Mayes, 1988; Milner, Petrides, & Smith, 1985; Moscovitch, 1989), monitoring of the veridicality and appropriateness of retrieved information (Moscovitch, 1989; Schacter, Norman, & Koutstaal, 1998), and the integration of successfully retrieved information into a coherent episode (Wilding & Rugg, 1996). Of course, these explanations are not mutually exclusive, and all of them may involve the common component of working memory (Cohen, Braver, & O'Reilly, 1996; Cohen & Servan-Schreiber, 1992; Kimberg & Farah, 1993; Norman & Shallice, 1986). Consistent with this view, right dorsolateral prefrontal and frontopolar activations have been observed in PET studies requiring the manipulation and monitoring of information within working memory (Bonda, Petrides, Frey, & Evans, 1995; Haxby, Ungerleider, Horwitz, Rapoport, & Grady, 1995; MacLeod, Buckner, Miezen, Petersen, & Raichle, 1995; Owen, Evans,

& Petrides, 1996; Petrides, Alivisatos, Evans, & Meyer, 1993a; Petrides, Alivisatos, Meyer, & Evans, 1993b). Further research is required to determine whether or not the link between the prefrontal cortex and episodic memory is secondary to a role in working memory.

Semantic Retrieval

Prior evidence that the left frontal cortex plays a central role in semantic retrieval, based on neuroimaging (Buckner, 1996; Buckner & Tulving, 1996; Nyberg et al., 1996; Tulving et al., 1994) and lesion studies (Benton, 1968; Butler et al., 1993; Milner, 1964), led us to predict a left frontal P3a reduction during semantic retrieval. Instead, in comparisons between semantic retrieval and tone-counting tasks, we found a right frontal P3a reduction. A smaller left frontal P3a reduction was also found, but it was not statistically significant.

There are several ways to interpret the contrast between our findings suggesting a right frontal contribution to semantic retrieval and neuroimaging and neuropsychological evidence emphasized a left frontal contribution. Other electrophysiological results have also been used to support left frontal involvement in semantic retrieval (Abdullaev & Posner, 1997; Abdullaev, Posner, Srinivasan, & Tucker, 1996; Snyder, Abdullaev, Posner, & Raichle, 1995). ERPs were compared between generating uses for nouns and a noun repetition baseline, as in prior PET studies (Petersen, Fox, Posner, Mintun, & Raichle, 1989; Raichle et al., 1994). In general, left-lateralized differences between the semantic retrieval task and the baseline task were found at selected anterior locations (although discrepant results were recently reported by Woldorff et al., 1998). Given these results, why did we see evidence of right frontal activation during semantic retrieval?

One explanation is that generating exemplars for categories versus verbs for nouns may not engage equivalent types of semantic retrieval. To begin with, nouns are generated in one case and verbs in the other. Neuropsychological studies have directly compared the relative roles of left frontal and temporal regions in the retrieval of verbs and nouns (Damasio & Tranel, 1993; Miceli, Silveri, Villa, & Caramazza, 1984). A double dissociation was observed, in that patients with left temporal lesions were more impaired at noun retrieval, whereas patients with left frontal lesions were more impaired at verb retrieval. When noun retrieval (category-exemplar naming) and verb retrieval (use generation) were compared using PET, verb retrieval was associated with a relatively greater left inferior frontal activation, and noun retrieval was associated with a relatively greater right superior frontal activation (Warburton et al., 1996). In another PET study, a condition in which participants monitored a sequence of nouns for names of dangerous animals was compared to a baseline condition in which they passively viewed nouns (MacLeod et al., 1995). Activation

during the semantic monitoring task was observed in the right prefrontal cortex and right frontopolar cortex, but not in left prefrontal regions. These results suggest a link between retrieval of nouns and right frontal activation.

Another possible interpretation of our findings of reductions in right frontal P3a amplitudes during retrieval is that they reflect an attentional rather than a memory effect. In other words, P3a may show a right frontal reduction whenever participants direct their attention away from auditory sequences, as in focusing on the visual modality to read the retrieval cues. If this were true, right frontal P3a reductions would be observed whenever participants direct their attention away from the novel sounds. However, this interpretation can be rejected on the basis of results from another study in which P3a was compared when novel sounds were attended or ignored (Friedman et al., 1998). Participants listened to a series of frequent tones, rare target tones, and novel sounds. In one condition, they paid attention to the sounds and pressed a button when they heard a rare target tone, whereas in another condition they ignored the sounds while reading text. Results showed that P3a was smaller when novel sounds were ignored than when they were attended and that these reductions were bilateral. In short, frontal P3a amplitudes are reduced when novel sounds are ignored, but the reduction is not specific to right frontal regions. Therefore, it is likely that the asymmetric right frontal P3a suppression that we observed reflected interference due to memory retrieval rather than merely shifting attention away from novel sounds.

The idea that right frontal regions may be engaged during both episodic and semantic retrieval is also supported by results from a recent functional magnetic resonance imaging study (Gabrieli et al., 1997). Comparisons were made across working memory, episodic memory, and visuospatial reasoning tasks, and similar right prefrontal regions were found to be activated during all three tasks. The authors speculated that “these areas may mediate a process that enhances attention to the products of internal thought as opposed to external perceptions and actions” (Gabrieli et al., 1997, p. 28). These results are consistent with our electrophysiological findings of similar patterns of right frontal activation during episodic and semantic retrieval.

Summary

To summarize, our results showed that task-induced suppressions of P3a can be used to measure frontal brain activation. In this context, ERPs can provide a source of information to complement other measures. Our results are consistent with neuroimaging findings suggesting that the right prefrontal cortex is more active than the left during episodic retrieval (Nyberg et al., 1996; Tulving et al., 1994). However, a straightforward mapping between retrieval of semantic and episodic memories and

the left and right prefrontal cortex, respectively, as in the HERA model, was not supported. Right frontal activation is apparently not specific to episodic retrieval. Further work using complementary electrophysiological and hemodynamic measures of brain activity is required to determine the precise functional significance of right frontal cortical activity in memory retrieval.

METHODS

Participants

Six men and six women, all right-handed and ranging from 17 to 34 years of age participated in the study. These participants were recruited through flyers posted in proximity to Northwestern University and were paid for their participation in the experiment.

Stimuli

Two lists of 20 cue phrases were generated by the experimenter, one for the episodic condition and one for the semantic condition. Cues for each condition are presented in Table 1. Although it is conceivable that identical category cues could have been used for both

Table 1. Cues for Episodic and Semantic Retrieval Tasks

<i>Episodic Task</i>	<i>Semantic Task</i>
Christmas	Presidents
Beach	Birds
Mother	European countries
Kitchen	Musical instruments
Amusement park	Universities
Driving	Green vegetables
Thanksgiving	State capitals
Birthday	Furniture
Movie	Colors
Shopping mall	Actresses
Grocery store	Clothing
Sporting event	Furry animals
Concert	Occupations
Fourth of July	Weapons
Graduation	Vehicles
Airport	Authors
Date	Trees
Doctor's office	Tools
Dinner	Basketball teams
Rain	Artists

tasks, it is unlikely that they would be equally effective in eliciting episodic and semantic memories. It was important that retrieval cues be effective enough so that participants would continue their retrieval attempts until the end of each trial. Therefore, cues were selected for the episodic and semantic retrieval tasks on the basis of pilot work indicating that they were effective at eliciting autobiographical memories and exemplars, respectively.

Seventy-five novel auditory stimuli were synthesized by modifying sound effects to last exactly 250 msec each. These sounds included samples of animal sounds, human voices, mechanical noises, and artificially generated waveforms. Some novel sounds may have been identifiable (e.g., the “moo” of a cow), but none contained a recognizable word. An auditory click sound (1-msec square wave) and a 250-msec tone (900-Hz pure tone) were also used. Sounds were presented at a constant rate of two per second.

Procedure

Each participant was fitted with an electrode cap (see below) and seated in a comfortable chair in a sound-attenuating chamber. Visual stimuli were presented on a monitor 140 cm away from the participant. Auditory stimuli were presented over speakers located on each side of the monitor. Participants were instructed to try to relax and to avoid blinking or moving while performing the experimental tasks.

The experiment consisted of four blocks, and each block consisted of 15 trials. Within each block, different tasks were assigned for the first 5, the second 5, and the third 5 trials. The order of the three tasks was counterbalanced across participants (see below), but for each participant the same task order was used in all four blocks. Each trial began with a fixation cross that was presented at the center of the screen for a minimum of 2 sec. After the experimenter determined that the EEG was artifact-free, the fixation cross was replaced by a visual cue that appeared at the center of the screen for the remainder of the trial. Cue phrases were presented in an uppercase yellow 48-point font on a black background and subtended a vertical visual angle of approximately 1°. Concurrent with the onset of the cue, the auditory sequence was initiated. This sequence included 20 clicks, 5 novel sounds, and from 1 to 5 tones. The sounds were presented in a pseudorandom order, with the provision that all sequences began with five consecutive clicks (see Figure 1).

For the *episodic retrieval task*, participants were instructed to use each cue to silently retrieve a detailed autobiographical memory. Participants were asked to retrieve as many details as possible about the event: when it happened, where it happened, the sights, sounds, smells, and so on. These instructions were based on findings from Johnson, Foley, Suengas, and Raye (1988) suggesting that levels of perceptual detail and temporal

context information are among the most salient factors differentiating imagined from real events. We felt that added emphasis on these factors would help to elicit recollective experiences closely tied to episodic memory (Tulving, 1972). Participants were told that there was no right or wrong answer, that the retrieved memory needn't be closely related to the cue, and that if more than one episodic memory was retrieved to choose the most recent. The chief requirement was to retrieve a memory of a single specific event, rather than a long period of time such as “the summer of 1994.” In the *semantic retrieval task*, participants were told that each cue would be a category name and that they were to silently retrieve as many members of the category as possible. The visual cue used for all trials of the *tone-counting task* was COUNT THE TONES and participants were instructed to keep a mental count of the number of tones in this condition.

Because a variable number of tones was presented in each trial, trial duration varied from 13 to 15 sec. After each trial in the episodic task, participants were asked to briefly describe the retrieved memory and to rate the memory for perceptual vividness on a four-point scale. The experimenter also inquired about the temporal context of the memory and rated it by assigning one point each for specifying the year, month, day, and approximate time. Thus a memory containing all this information (e.g., “last Friday I went to the movies at 6 p.m.”) would receive a 4 on this scale, whereas a memory without temporal context information (e.g., “when I was a kid we went to Disneyland”) or a nonspecific memory (e.g., “we used to spend our summers in Nantucket”) would receive a zero. After each trial in the semantic task, participants listed at least four of the exemplars just retrieved. After each trial in the tone-counting task, participants stated the number of target tones counted.

Counterbalancing

The order of the three tasks was counterbalanced across participants to reduce the influence of order effects (using each of the six possible orders). The first block included 75 unique novel sounds presented with tones and clicks in the same random order for each participant. A different random order of the same stimuli was used in each subsequent block. Thus, one-third of the participants heard five novel sounds in block 1 while performing the episodic task, one-third heard the same sounds in block 1 while performing the semantic task, and one-third heard the same sounds in block 1 while performing the tone-counting task. Across participants, each novel sound occurred equally often in each task.

ERP Methods

Electroencephalographic recordings were made from 21 scalp electrodes (Fpz, Fz, Cz, Pz, Oz, Fp1, Fp2, F3, F4, F7,

F8, C3, C4, P3, P4, O1, O2, T3, T4, T5, T6) imbedded in an elastic cap. Electrooculographic (EOG) recordings were made using an electrode below the right eye (vertical EOG) and electrodes lateral to each eye (horizontal EOG). Scalp electrode impedances were 5 k Ω or less. The band pass was 0.1 to 100 Hz. Scalp and vertical EOG electrodes were referenced to a left mastoid electrode during recording and the reference was changed to the average of the left and right mastoid recordings off-line. Trials with artifacts due to blinks or eye-movements were excluded prior to averaging. Also, trials during the episodic retrieval task were rejected if participants did not successfully retrieve an autobiographical memory, and trials during the semantic retrieval task were rejected if participants did not successfully retrieve four exemplars. Across conditions, the mean percentage of rejected trials was 9.6%. In statistical analyses, the Huynh-Feldt correction was used where appropriate.

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