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Event-Related Potential (ERP) Studies of Memory Encoding and Retrieval: A Selective Review

DAVID FRIEDMAN[1]* AND RAY JOHNSON, JR.[2]
[1]*Cognitive Electrophysiology Laboratory, NY Psychiatric Institute, New York, New York 10032*
[2]*Department of Psychology, Queens College of CUNY, Flushing, New York 11367*

ABSTRACT As event-related brain potential (ERP) researchers have increased the number of recording sites, they have gained further insights into the electrical activity in the neural networks underlying explicit memory. A review of the results of such ERP mapping studies suggests that there is good correspondence between ERP results and those from brain imaging studies that map hemodynamic changes. This concordance is important because the combination of the high temporal resolution of ERPs with the high spatial resolution of hemodynamic imaging methods will provide a greatly increased understanding of the spatio-temporal dynamics of the brain networks that encode and retrieve explicit memories. *Microsc. Res. Tech. 51:6–28, 2000.* © 2000 Wiley-Liss, Inc.

INTRODUCTION

The goal of specifying the cognitive and neuroanatomical underpinnings of memory has long interested psychologists and neuroscientists. The advent of techniques that measure blood flow (all of the functional imaging studies reviewed here are concerned with measures of blood flow, i.e., hemodynamic, and not glucose metabolism or other metabolic processes) during cognitive processes, as attested to by many of the papers in this volume. Such studies have brought a much greater understanding of which brain areas are recruited during the formation and retrieval of explicit memories. However, because the hemodynamic response peaks between 5 and 10 seconds following the stimulus, these techniques are relatively slow compared to the processes involved in forming and retrieving memories. For example, in positron emission tomography (PET) scanning, hemodynamic data are accumulated over some 30–60 seconds during which subjects are processing different kinds of stimuli, perhaps in different ways and with different processing strategies. Standard functional magnetic resonance imaging (fMRI) has many of the same problems as the PET technique, although newer event-related fMRI procedures eliminate some, but not all, of these problems. Thus, in spite of their high spatial resolution, the relative slowness of the hemodynamic response is a major shortcoming of all blood flow measures.

Event-related brain potentials (ERPs), on the other hand, have a temporal resolution in the millisecond (ms) range that permits the precise quantification of the temporal characteristics of neural activity. The major disadvantage of the ERP method is the inability to unequivocally determine the locations of the neural generator(s) responsible for the scalp-recorded ERP components. Nevertheless, the use of larger electrode arrays, combined with spatial filtering techniques, can provide a more detailed view of cortically generated activity.

The current review is based only on ERP mapping studies of encoding and retrieval of explicit memory (i.e., those that relate spatio-temporal patterns of scalp-recorded neural activity to particular tasks). Restricting the review in this way reflects our belief that one can only acquire the fullest information regarding the cognitive and neuroanatomical bases of memory by combining the temporal and spatial information available from dense electrode arrays (i.e., large numbers of electrodes). Readers interested in more complete reviews of the ERP memory literature up to 1995 are directed to R. Johnson (1995a) and M.D. Rugg (1995). Finally, this review is also restricted to young adult participants. Overviews of age-related ERP and functional imaging findings can be found, respectively, in Friedman (1995, in press) and Grady (1998, in press). Whenever possible, we have integrated ERP results with spatial information available from comparable PET and fMRI investigations. Our review of the hemodynamic studies will also be highly selective, with only those results that have been consistently replicated in tasks comparable to those used in ERP studies.

SCALP-RECORDED EVENT-RELATED BRAIN POTENTIAL

ERPs are voltage changes induced within the brain in response to a variety of sensory, cognitive, and motor processes. The ERP consists of a sequence of positive and negative voltage fluctuations that are labeled components. These components are identified with various sensory, cognitive (e.g., retrieval) and motor processes based on their scalp distribution and response to experimental variables. Moreover, ERP components are

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*Correspondence to: David Friedman, Ph.D., Cognitive Electrophysiology Laboratory, New York Psychiatric Institute, Unit 6, 1051 Riverside Drive, New York, NY 10032. E-mail: df12@columbia.edu

*Correspondence to: Ray Johnson, Jr., Ph.D. Department of Psychology, Queens College of CUNY, Kiseena Boulevard, Flushing, NY 11367. E-mail: Ray_Johnson@qc.edu

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useful as measures of covert information processing, as differences between conditions can be obtained in the absence of behavioral responding (e.g., encoding).

Although these ERP signals are small (1–30 millionths of a volt), and are embedded in electroencephalographic (EEG) activity unrelated to the eliciting event, they can be recorded non-invasively from the scalp by means of signal averaging techniques. In other words, the more trials (of a given type) one includes in an average, the greater the reduction in the non-stimulus related EEG activity (i.e., noise). The number of trials required to produce a noise-free ERP is highly variable because this number is dependent on the size (i.e., signal-to-noise ratio) and period (i.e., the component's frequency) of the ERP component of interest. It is worth noting that many cognitive ERP components are large and overlap little with the frequencies of the waking EEG so that averages with good signal-to-noise ratios can be generated on the basis of relatively few trials (e.g., 15–30). Another advantage of the ERP technique is the ability to use experimental designs in which the presentations of all stimulus categories can be completely randomized.

There are three measurable aspects of the ERP waveform, amplitude, latency, and scalp distribution (Johnson, 1992). While component amplitude provides an index of the extent of neural activation (i.e., how the component responds functionally to experimental variables), component latency (i.e., the point in time at which the peak occurs) reveals the timing of this activation. Finally, a component's scalp distribution (i.e., the pattern of voltage gradient over the scalp at any point in time) provides information on the overall pattern of activated brain areas. One caveat is that, to be recorded at the scalp, the neural generators of the ERP must have the appropriate configuration and orientation with respect to the scalp (see Picton et al., 1995). Therefore, the presence of two sequential components in the ERP waveform does not necessarily indicate sequential stages of processing. That is, it is possible that additional, intervening stages are present, but the generators that give rise to these activities do not have the appropriate orientation (Johnson, 1992). Because each neural generator has a positive and negative pole, the polarity of an ERP component is primarily a reflection of the relation between electrode position and the orientation of the intracranial generator.

A disadvantage of the ERP technique is its relatively poor spatial resolution, which typically requires complex modeling in order to determine the locations of the generators of scalp-recorded potentials (see Wikswo et al., 1993). Some source localization methods appear to be more viable than others (see Koles, 1998, for an extended discussion) and localization solutions for some ERP components, such as the primarily sensory-related waveforms, are extremely good (e.g., Gevins et al., 1999; Miltner et al., 1994). Note that one way to use source localization is to "seed" the coordinates of activated brain regions generated in comparable PET or fMRI studies, and determine which aspects of the ERP can be explained by a source(s) in that location (e.g., Heinze et al., 1994; Menon et al., 1997; Opitz et al., 1999a,1999b). One caveat to this approach is that the relation between the neural activity from the ERP and the sites of increased blood flow has not been definitively established. An alternative approach is to infer the generators of ERP components from studies of patients with localized brain injuries (Knight and Nakada, 1998) or from electrodes implanted intracranially (e.g., Elger et al., 1997; Fernandez et al., 1999; Guillem et al., 1999).

Despite the difficulties of determining the generator sites of specific ERP components, the scalp distribution of the ERP can provide extremely useful and complementary information to component amplitudes and latencies. Comparison of the scalp distributions of ERPs elicited by different stimuli, either within or across conditions, allows one to infer whether the two stimuli engage different patterns of neural activity and, hence, reflect different functional processes (see R. Johnson, 1993, for a review and caveats). Hence, by combining the temporal and spatial information available in the ERP waveform recorded over a large number of different areas of the scalp, it is possible to determine the temporal characteristics (both onset and duration) of stimulus- and condition-specific patterns of brain activity.

When recording from large arrays of electrodes, the easiest and clearest way to represent the data is with maps. At present, two types of maps can be generated for any given data set, voltage and current source density (CSD). While both types of maps are derived directly from the original amplitude data, they each provide very different views of the brain's activity (for a complete tutorial, see Picton et al., 1995). This is because the scalp-recorded ERP activity reflects the summation of all the neural activity, both cortical and subcortical, during any given temporal window. An essential difference between these mapping methods is that they differentially weight the contribution of subcortical activity. Because voltage maps are derived from the ERP amplitudes obtained at each electrode site, they provide a means of visualizing the summed activity from *all* active brain areas. By contrast, before CSD maps are calculated, the amplitudes are spatially filtered with an algorithm that removes the activity volume conducted from subcortical and distant cortical areas. The resulting maps provide a spatially-sharpened, reference-free display of positive and negative current densities that emphasize local (i.e., cortical) differences (Nunez, 1981; Picton et al., 1995). Because local generators are represented by this technique, CSD maps are particularly useful for forming hypotheses about neural sources in superficial cortex (Perrin et al., 1989). Note that, for both types of maps, the mapping algorithms take the ERP waveform voltages from all of the discrete recording sites and interpolate between them to yield a continuous distribution of amplitudes across the scalp. As the appearance of positive and negative current densities in these maps is dependent on the orientations of the neural generators, their meaning cannot be unequivocally determined (see Picton et al., 1995, for a complete discussion). Generally, however, there is no need to interpret such information because one is only concerned with when different conditions are characterized by different patterns of positive and negative current densities.

The differences between the voltage and CSD mapping techniques suggest that it is generally best to calculate both types of maps for a given data set. This is because, while CSD maps allow one to infer neocortical sources implicated in memory function, the activity of deeper generators, such as the hippocampus, would only be revealed in the voltage maps. Unfortunately, CSD mapping techniques are not yet widely employed and therefore the majority of scalp distribution comparisons presented below used voltage maps. It is important to note that all maps are visual aids only and do nothing to quantify the activity patterns they display. Thus, topographic analyses (i.e., quantification of scalp distribution differences) must still be done on the ERP amplitudes in order to determine if the differences revealed by the maps are significant. Possible topographic differences are revealed by significant interactions between the experimental effects and the electrode factor in an ANOVA. To ensure that the comparisons are confined to shapes alone, and not amplitude differences, the data are first scaled so that the between-condition amplitude differences are removed (for extended discussions see Johnson, 1993; Ruchkin et al., 1999).

Overview of Memory

Long-term memory is generally viewed as consisting of a collection of separate but interacting systems that comprise two broad categories: explicit and implicit (Cohen and Squire, 1980). The explicit category refers to consciously recollected memories while the implicit category refers to a collection of highly specialized stores whose contents do not require conscious access. Explicit memory has been subdivided further into episodic and semantic stores, with the former consisting of personal memories that include specific spatio-temporal information about the context in which the event occurred (Tulving, 1984). Semantic memory, in contrast, consists of a fact-based store for general knowledge that is not associated with contextual information.

Retrieval of episodic memories is often assessed with tests that make direct reference to a previous learning episode (e.g., recognition, recall). For recognition tests, subjects are exposed to a series of items and, after some delay, are tested with lists that include these "old" items randomly intermixed with new items. The subject's task is to decide whether each item is old or new. Recall tests require subjects either to generate the old items with no cue (free recall) or from a fragment of the item (cued recall). Thus, while recall is generally more difficult than recognition, these two retrieval tasks differ in the extent to which subjects must generate their own information about items already in memory. In contrast to the large number of behavioral studies, relatively less is known about the brain systems underlying each type of retrieval.

STUDIES OF ENCODING

Behavioral studies have demonstrated several basic phenomena about the relations between the processes used during encoding and successful retrieval. For example, depth of processing investigations have shown that deeper encoding leads to better retrieval performance than shallow encoding (e.g., Craik and Lockhart, 1972). That is, stating whether a concept (e.g., a word or picture) represents a living or non-living item (i.e., semantic encoding) produces better recognition and recall performance than stating whether the word contains any T-junctions (i.e., orthographic encoding). Brain imaging studies (reviewed below) have begun to reveal the neuroanatomical bases of these encoding processes. For example, one brain region that appears to be particularly important to successful encoding is the left inferior prefrontal cortex. Another encoding phenomenon, labeled transfer appropriate processing, states that items are better remembered when the processes engaged in during retrieval are the same as those engaged in during encoding (e.g., Roediger and McDermott, 1993).

In addition, other investigators have shown that deep or semantic processing leads to a greater proportion of "remember" (retrieval based on context, presumably enhanced by semantic encoding; i.e., a recollective response) responses, whereas shallow processing leads to a greater proportion of "know" responses (engendering only a feeling of familiarity with the item; Tulving, 1985). Because these two types of retrieval have been linked to different states of awareness, it is reasonable to assume that they should have separable neural configurations (e.g., Henson et al., 1998). Further, if different neural circuits are recruited during retrieval, then the foundation for those differences should be formed during encoding.

ERP Results

Like behavioral investigators, ERP researchers have also used depth of encoding manipulations to quantify the brain activity elicited during memory acquisition. For example, the ERP activity elicited when subjects were asked to make living/non-living judgments about a series of pictures of objects followed by a speeded reaction time (RT) response is shown in Figure 1 (Johnson, unpublished observations). This prototypical deep encoding task requires subjects to retrieve semantic information about each object to perform the classification task. As shown in Figure 1, CSD maps were computed for three sequential 200-ms intervals of the waveforms, beginning at 410 ms. A prominent aspect of these maps is the large negative current density over left inferior frontal scalp between 410 and 800 ms. The timing and duration of this neural activity roughly corresponds to the interval during which subjects were making their semantic judgments as measured by RT (mean = 542 ms; SD = 140 ms). This area of inferior prefrontal ERP activity corresponds well to locations of activation that have been reported during PET and fMRI investigations of both episodic encoding and semantic retrieval tasks (e.g., Gabrieli et al., 1998; Thompson-Schill et al., 1997).

One advantage of the ERP technique over those imaging methodologies that require blocking of conditions that is of particular relevance to encoding studies, is the ability to sort the responses to individual stimuli in any way that is behaviorally relevant. For example, rather than being limited to simply averaging across all stimuli being encoded, it is possible to sort encoded items on the basis of whether they are remembered in a subsequent memory test. In this way, experimenters can quantify the differences in neural activity that are associated with individual items that are or are not to be subsequently remembered. Unfortunately, the early ERP studies of encoding phenomena did not have suf-

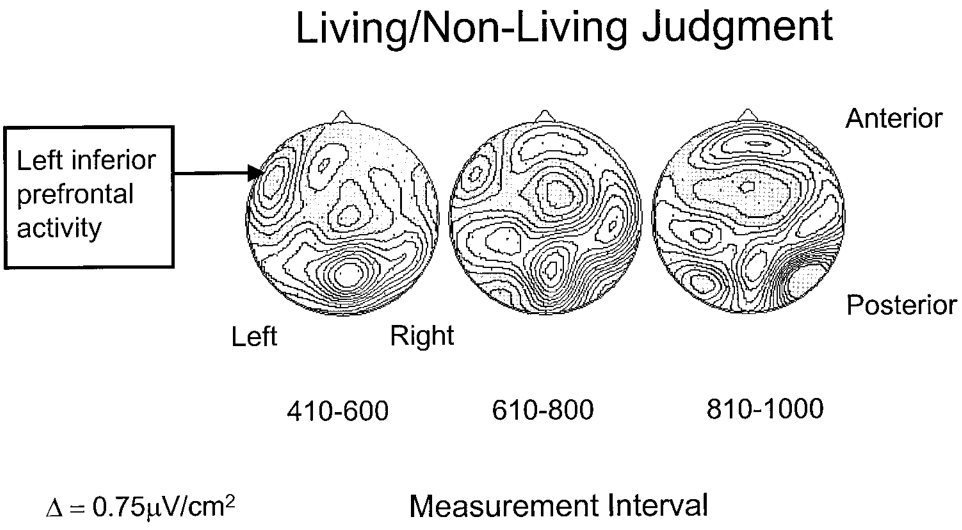

Fig. 1. Current source density maps during a task in which subjects made living/non-living semantic judgments about pictures (Johnson, unpublished observations). In this, and all subsequent figures, the maps should be viewed like any contour map, with shaded areas indicating negativity, and unshaded areas positivity. All maps are oriented such that the views are of the top of the head with anterior regions at the top of the page and posterior regions at the bottom; left hemiscalp is on the left and right hemiscalp on the right.

ficient coverage of the scalp to identify these kinds of anatomically specific effects. As reviewed below, however, that situation has improved and a measure of consistency between the ERP and hemodynamic studies has resulted.

In a seminal study, Sanquist and colleagues (1980) addressed the issue of neural differences during encoding as a function of subsequent retrieval. They observed that the ERPs elicited by study items that were subsequently recognized elicited larger positive amplitudes over midline parietal scalp than those that were subsequently missed. They further reported that this effect appeared greater for items studied during a semantic orienting task compared to items studied during an orthographic encoding task. In a subsequent investigation, Paller et al. (1987) isolated this difference in brain activity by subtracting the ERPs elicited by study items subsequently forgotten (i.e., Misses) from the ERPs elicited by study items subsequently remembered (i.e., Hits). They labeled this differential, parietal-maximal, brain activity, "Dm," for Difference in Subsequent memory. These, and other early studies with similar results, recorded from only a few midline scalp sites and, therefore, could not have observed left inferior prefrontal activity.

Recently, however, the nature of brain differences during encoding as a function of subsequent memory performance has been mapped (Friedman and Trott, unpublished observations). Subjects were asked to memorize two unassociated nouns embedded in sentences for a subsequent recognition test (described in detail in Friedman and Trott, 2000; Trott et al., 1999). The resulting waveforms elicited by study items categorized according to subsequent memory performance are depicted in Figure 2A. Here it is evident that, during encoding, items that were subsequently recognized (Hits) elicited greater positivities in the interval between 400–1,100 ms than words that were subsequently unrecognized (Misses; Fig. 2A). The subjects in Friedman and Trott's (2000) investigation likely processed at least some of the semantic content of the sentences in which the nouns were embedded. Consistent with the idea that left prefrontal activation is important for efficacious encoding, there is a negative current density over left inferior prefrontal scalp evident in the CSD maps for both temporal windows depicted in Figure 2C (500–800; 810–1,100 ms). If the apparent congruence between the ERP and hemodynamic data can be confirmed, the data suggest that the neural events leading to the hemodynamic activations observed in PET and fMRI studies (e.g., Thompson-Schill et al., 1997) begin at about 400 ms and are prolonged for approximately 1 s. Another indication of the distributed nature of the encoding activations is suggested by the comparison of the voltage (top row) and CSD maps (bottom row) in Figure 2C. The CSD and voltage maps show areas of widespread, but different, patterns of activity, a finding indicating that deeper structures most likely contribute to the Dm effect recorded at the scalp. While it is impossible to determine from scalp distributions alone which deep structures are contributing, it is worth noting that Fernandez et al. (1999; see below) have found Dm-like activity in the hippocampus using indwelling electrodes. Note also that in Figure 2C there is evidence of parietal scalp activity. Taken together, the fact that Dm effects have been observed at midline parietal scalp, over left inferior prefrontal scalp and subcortically, suggests that these subsequent memory effects are engendered by a widespread network of brain areas.

ERP investigators have also used the remember/know technique to assess the effect of differential encoding processes as a function of subjects' awareness of the subsequently retrieved item. For example, Friedman and Trott (2000) reasoned that, if a Remember response indicates that an item has been retrieved along with its context and a Know response reflects familiarity-based retrieval, these differences should be evident during encoding. As predicted, differences in the amplitude of the Dm effect as a function of type of judgment given at test were found (see Fig. 3). The ERPs elicited by study items that were associated subsequently with Remember judgments showed greater

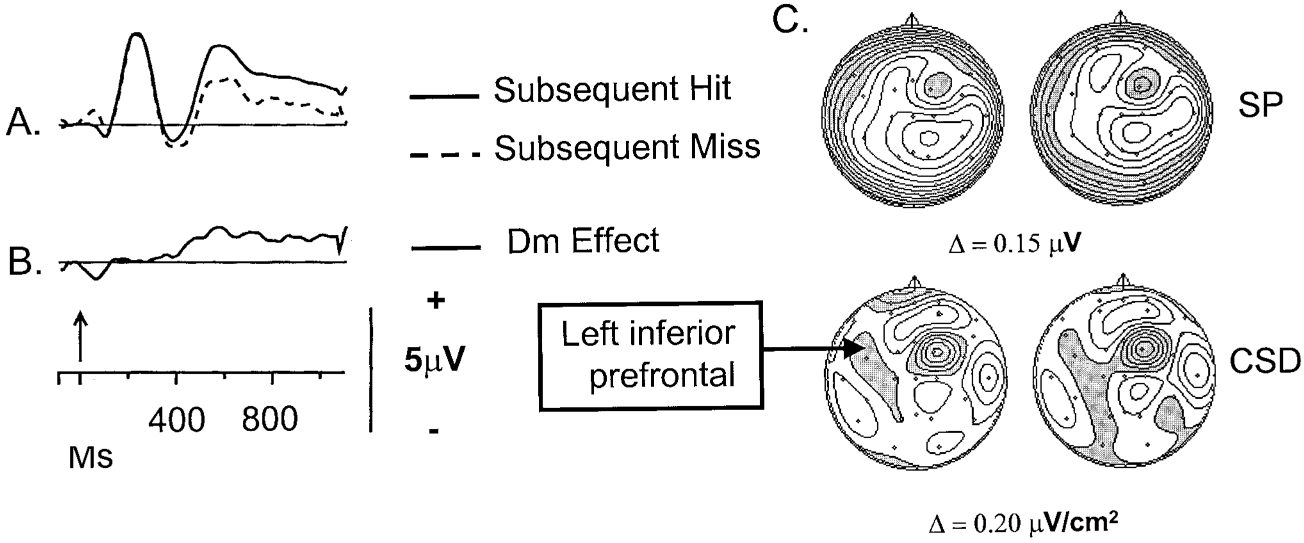

Fig. 2. **A:** Grand mean ERPs elicited by study items that were (Hit) or were not (Miss) subsequently recognized. **B:** Grand mean Dm effect, i.e., difference waveform obtained by subtracting the subsequent miss waveform in A from the subsequent Hit waveform in A. **C:** Voltage or Surface Potential (SP; first row) and current source density (CSD; second row) maps for two measurement windows (500–800; 810–1,100 ms) for the ERP data depicted in B. Data in A and B recorded at a left inferior prefrontal scalp site.

amplitude from about 400 to 1,100 ms than those that were subsequently missed. In contrast, ERPs to study items subsequently associated with Know judgments did not differ reliably from the ERPs to study items that were subsequently missed. Furthermore, the CSD maps for the same 2 intervals as in Figure 2C (500–800; 810–1,100 ms) show that items that will be subsequently given a Remember judgment are associated with left inferior prefrontal scalp activity (arrow in Fig. 3C), supporting the idea that the processes that will engender a Remember or a Know judgment are operative during encoding. Note that the left inferior prefrontal scalp activity is of greater magnitude in Figure 3C compared to Figure 2C. That is because the maps depicted in Figure 3C are based on only those study items that would be subsequently associated with a Remember judgment, whereas those in Figure 2C are based on all subsequently correctly recognized trials. However, as is evident from the data in Figure 3, the Dm effect is evident for those items given a subsequent Remember judgment, and not for those associated with a subsequent Know judgment.

Mangels and colleagues (unpublished observations) assessed ERP subsequent memory effects to determine if they would differ as a function of the amount of episodic information that would be subsequently retrieved. Mangels et al. (unpublished observations) computed Dm effects to items that would be (1) subsequently correctly recognized, given a Remember judgment and freely recalled (RR trials), (2) subsequently correctly recognized, given a Remember judgment, and not freely recalled (RO trials), (3) subsequently correctly recognized and given a Know judgment (K trials), and (4) subsequently forgotten or missed (M trials). Like Friedman and Trott (2000), they found a long-lasting, positive-going slow wave (1,000–2,000 ms) whose amplitude was directly related to the amount of retrieved episodic information (i.e., RR > RO > K = M). Unlike Friedman and Trott (2000), they reported that an N400-like component (peaking at about 400 ms and sensitive to semantic attributes of stimuli) maximal over left inferior temporal scalp (T7) also predicted which items would be subsequently recognized. However, N400 amplitude did not differ as a function of the amount of episodic information that would be subsequently retrieved (i.e., [RR = RO = K] > M). One speculative interpretation of these data is that this early encoding effect is a correlate of familiarity, enabling an item to be subsequently recognized but without contextual detail. On this view, the later, positive-going sustained activity would reflect elaborative processing of the kind that would engender subsequent recognition with associated contextual details.

Given that some of the Dm effect appears to be of subcortical origin, more precise localization information may be obtained from patient studies. Recent results on Dm obtained from intracranial recordings are in good agreement with the temporal information provided by the scalp-recorded ERP data. For example, Fernandez et al. (1999) recorded ERPs from medial temporal lobe (MTL) structures as pre-surgical temporal lobe epilepsy patients studied single words for a subsequent free recall memory task. The ERPs to study words were averaged as a function of subsequent recall performance. Within the anterior parahippocampal cortex, an N400-like potential was larger to subsequently recalled than unrecalled words (the divergence began at about 300 ms), highly similar to that observed in the scalp-recorded data of Mangels et al. (2000). Within the hippocampus, the Dm effect took the form of a positive-going potential with the subsequently recalled and unrecalled waveforms diverging at about 500 ms post-stimulus. Due to local polarity reversals within the anterior parahippocampal cortex and steep current gradients within the hippocampus, Fernandez and colleagues (1999) concluded that both the N400-

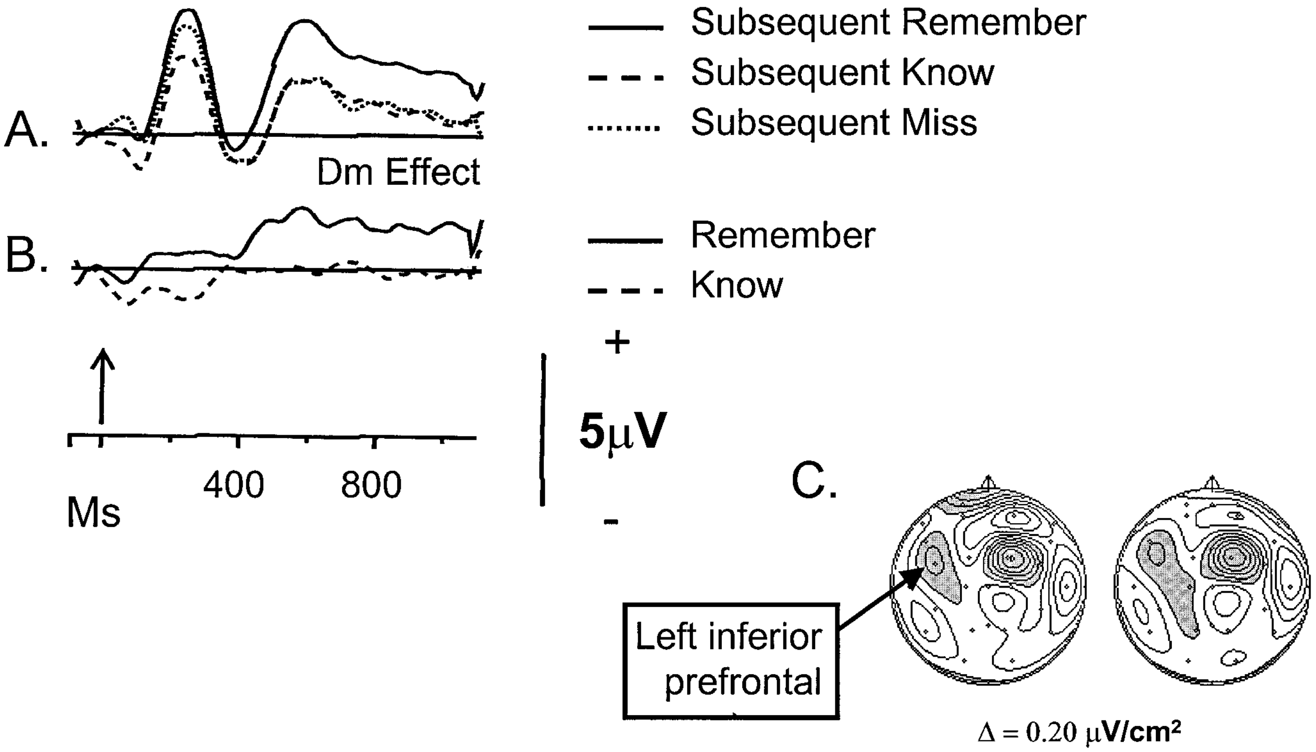

Fig. 3. **A:** Grand mean ERPs elicited by study items that were subsequently associated with remember or know judgments (hits) or were unrecognized (misses) during the subsequent recognition test. **B:** Grand mean difference waveforms computed by subtracting the ERPs to study items subsequently missed from those that were subsequently associated with either a remember or know judgment (Modified from Friedman and Trott, 2000). **C:** CSD maps for 2 intervals (500–800; 810–1,100 ms) measured in the Dm waveform associated with a subsequent Remember judgment. Data in A and B recorded at a left inferior prefrontal scalp site.

like and Dm activity were generated within these respective structures. Recordings from strip electrodes in the vicinity of Wernicke's area did not differentiate subsequently recalled from unrecalled items, suggesting that the Dm effects were specific to MTL structures.

Elger and colleagues (1997) also attempted to localize Dm-like activity by recording from lateral and anterior MTL placements in pre-surgical temporal lobe epilepsy patients. They used word and picture continuous recognition memory paradigms that interpose study and test trials within the same series of stimuli. The amplitude of N400-like ERPs elicited by words in the middle temporal gyrus of the dominant left hemisphere was correlated with immediate recall performance that followed the continuous recognition task, whereas N400 amplitudes elicited by words but not pictures in the left anterior MTL were correlated with subsequent delayed recall performance. This is obviously not the typical subsequent memory or Dm effect. Nevertheless, these data are generally consistent with those of Fernandez et al. (1999) in demonstrating correlations with subsequent memory performance in structures that are critical for explicit memory performance.

Aggleton and Brown (1999) have advanced the intriguing hypothesis that the perirhinal cortex subserves familiarity (sufficient to make Know judgments), whereas the hippocampus proper is responsible for episodic retrieval (Remember judgments). The scalp- and intracranially-recorded ERP data reviewed above could lend some credence to this notion, as the early negativity (N340) of Mangels et al. (2000) did not differentiate ERPs elicited by items that would subsequently attract Remember judgments from those that would attract Know judgments, but was recorded in areas outside the hippocampus proper (Fernandez et al., 1999). On the other hand, the slow positivity during encoding was sensitive to recollective processing (Friedman and Trott, 2000; Mangels et al., unpublilshed observations) and was recorded from within the hippocampus proper (Fernandez et al., 1999). However, at the current time there are too few data to reach a definitive conclusion.

Integration of Encoding ERP and Hemodynamic Results

In summary, ERP investigators have demonstrated the presence of different but overlapping patterns of brain activity for manipulation of depth of processing and subject awareness during encoding. Based on the admittedly limited data, the common area that is active for both of these manipulations is left inferior prefrontal scalp. Consistent with behavioral studies, Dm activity is greater when semantic processing is required at encoding, and this may be the reason why this activity is present for study items that are subsequently given a Remember judgment. To date, however, there are no studies (to our knowledge) incorporating the transfer appropriate processing methodology, and the application of mapping techniques to ERP studies of encoding has yet to be fully implemented.

Based on the available data, there appears to be good congruence between the results of both ERP and hemodynamic studies of the brain activity underlying episodic encoding processes. For example, the HERA model (Hemispheric Encoding Retrieval Asymmetry) postulates that, during encoding, left inferior prefrontal cortex is activated due to the semantic retrieval processes engaged whenever subjects encoded items for a subsequent memory test (Tulving et al., 1994). This early finding has been replicated and extended in a variety of subsequent studies (for a recent review see Gabrieli et al., 1998). However, based on a recent series of studies, Thompson-Schill and her collaborators (Thompson-Schill et al., 1997, 1999) have suggested that this left inferior prefrontal cortex activation is due to processes involved in the *selection* of appropriate responses from among competing alternatives, rather than to semantic retrieval per se. In their view, left inferior prefrontal cortex plays more of a supervisory, non-semantic role, while temporal cortex is more directly involved in retrieving semantic information. The lack of sufficiently precise timing information in the PET and fMRI methods (whether blocked or event-related) makes it more difficult to evaluate the relative merits of these competing hypotheses. For example, as selection of appropriate responses must occur after semantic retrieval, knowing the onset time and duration of left inferior prefrontal cortex activation would support only one of these hypotheses. The comparable ERP data from a study that used semantic encoding manipulations (Fig. 1) clearly showed left inferior frontal scalp activity. Moreover, the fact that the duration of this brain activity straddled the RT response indicating semantic retrieval is consistent with the idea that this area is involved both in semantic retrieval and episodic encoding (Johnson unpublished observations). Further, both this and the Friedman and Trott (2000) study also showed activity over the temporal lobes, an area where imaging studies also show consistent activations (see Cabeza and Nyberg, 1997).

PET and fMRI investigations of encoding have also confirmed the results of previous patient studies on the importance of MTL structures, particularly the hippocampus in the formation of episodic memories (Schacter and Wagner, 1999). Lepage and colleagues (1998) concluded that the anterior MTL was activated during encoding while the posterior portion was activated during retrieval. However, based on their reanalysis of the same data, Schacter and Wagner (1999) concluded that this anterior/posterior distinction could not account parsimoniously for all the data. The intracranial data of Fernandez et al. (1999) are consistent with these findings as they found Dm-like activity in anterior parahippocampal cortex. Moreover, the ERP data shed light on the timing of these activations. For example, Fernandez et al. (1999) found that, beginning around 500 ms, the ERPs were larger to subsequently recalled than unrecalled words. In agreement with this, the scalp-recorded data (Fig. 2) revealed that the ERPs elicited by subsequently correctly recognized items diverged from those for subsequently missed items as early as 400 ms post-stimulus. This suggests that within this time period, stimulus features that will subsequently distinguish remembered from forgotten items have been encoded by the brain. Moreover, although difficult to localize on the basis of scalp-recorded ERP data alone, the convergence of imaging and intracranial ERP data implicates MTL structures in the generation of the Dm effect, a hypothesis first advanced by Johnson (1995a).

Two recent studies using event-related fMRI and the Remember/Know procedure allow a strong basis for comparing the results from fMRI and ERP studies (Brewer et al., 1998; Henson et al., 1998; see also Wagner et al., 1998 for an event-related fMRI study of encoding and retrieval that did not include remember/know judgments). Brewer and colleagues (1998) recorded event-related fMRI responses to pictorial study items (during a semantic encoding task) as a function of whether they would be associated with Remember or Know judgments, or whether they would be forgotten (i.e., missed) during the subsequent test phase. The hemodynamic response in bilateral parahippocampal cortex and right (but not left) prefrontal cortex was larger to study items subsequently associated with remember judgments compared to study items subsequently associated with know judgments, and both these responses were larger than that to study items that were subsequently forgotten. However, inspection of figure 3 from Brewer et al. (1998) suggests that, at right prefrontal regions, the difference between the hemodynamic response to study items associated subsequently with Remember judgments and those subsequently missed is much greater than the difference between the hemodynamic responses associated subsequently with Know judgments and those subsequently missed. This latter observation is highly similar to the results of the Friedman and Trott (2000) study described above, in which the Dm effect was much larger to items subsequently given a remember judgment. Similar to Brewer et al. (1998), Friedman and Trott (2000) observed positive right prefrontal current densities in maps of Dm activity. However, unlike Brewer et al. (1998), whose temporal information is quite limited, the Friedman and Trott (2000) data suggest that this right prefrontal activity onsets as early as 500 ms following the presentation of the to-be-encoded item.

In the second event-related fMRI investigation of the remember/know paradigm, Henson and colleagues (1998) used a lexical decision task during the encoding phase, ensuring that study items would be processed for their semantic attributes. Areas in left (but not right) prefrontal cortex predicted which items would be subsequently recollected compared to those that would be recognized based on familiarity. The difference in asymmetry of the prefrontal activations between Henson et al. (1998) and Brewer et al. (1998) could be due to differences in stimulus materials, verbal items for Henson et al. (left-sided asymmetry) and pictorial for Brewer et al. (right-sided asymmetry). Henson et al. (1998) did not compute hemodynamic responses at study as a function of whether the items would be subsequently forgotten so they did not have a baseline with which to compare the blood flow responses subsequently associated with remember and know judgments. This prevents direct comparison between the

Friedman and Trott (2000), Brewer et al. (1998), and Henson et al. (1998) studies. Nonetheless, the Henson et al. (1998) results are in broad agreement with the ERP (Friedman and Trott, 2000) and fMRI (Brewer et al., 1998) investigations in showing a large difference between study items subsequently associated with remember compared to know judgments. Another way in which the ERP and fMRI results overlap is Henson et al.'s (1998) finding of left precuneus activation during study to items that would be subsequently given a Remember judgment. This activation may correspond to the parietal maximal Dm effects that have been recorded by many investigators (see review by Johnson, 1995a).

STUDIES OF RETRIEVAL

Recognition of episodically stored material has most often been modeled as consisting of two distinct processes. Such dual-process models, as they are known, postulate that a familiarity or "perceptual fluency," as well as a contextual episodic component contribute to recognition judgments (Atkinson and Juola, 1973; Jacoby and Dallas, 1981; Mandler, 1980). That is, these models attempt to explain the fact that one may recognize a person's face while being completely unable to remember the person's name or where (spatial) and when (temporal) they were seen last. Hence, the main difference between these two processes is that recollection involves retrieval of contextual information specific to the study episode while familiarity does not. Mandler (1980) argued further that familiarity is an automatic (unconscious) process while recollection is a controlled (conscious) process, while Jacoby (1991) has associated them with implicit and explicit memory processes, respectively. According to this conceptualization, recollection, but not familiarity, should depend on MTL structures (i.e., hippocampal), as they are key brain regions in the explicit memory system (Squire, 1992).

It should be noted, however, that familiarity-based processes may not be equivalent to implicit memory. For example, recent patient data suggest that residual recognition memory performance by amnesics with MTL damage is not likely due to familiarity engendered by an "implicit" memory mechanism (Reed et al., 1997). Furthermore, Knowlton and Squire (1995) demonstrated that "know" responses (presumably evidence of implicit, familiarity-based recognition) depend upon the structures damaged in amnesia (i.e., MTL and/or diencephalic regions). Therefore, in the remainder of this review we will use the term familiarity to refer to the explicit mechanism only.

ERP RESULTS (RECOGNITION): THE EPISODIC MEMORY (EM) EFFECT

The majority of ERP memory studies have investigated the neural basis of explicit recognition and recall, and have demonstrated differential ERP responses depending on the study status of the item being recognized. In such recognition memory paradigms, processing new words accesses semantic memory whereas processing old words, having been experienced previously, accesses episodic memory. As characterized previously, old words elicit a larger late positive component (LPC) over parietal scalp in the interval between 400–800 ms than do new words (for reviews see Johnson, 1995a; Rugg, 1995). In addition, old words reliably elicit earlier parietal LPCs (Johnson et al., 1985; Neville et al., 1986) and shorter RTs (Johnson et al., 1985) than unstudied words (although for an exception see Cycowicz et al., unpublished observations). The greater amount of LPC activity elicited by old words, which has been referred to as the parietal old/new effect, has a scalp distribution that is asymmetrical for verbal stimuli, being larger over left parietal electrode sites. Because the term "old/new" describes how the ERP difference is isolated rather than the meaning of the difference, we believe that the differential ERP activity elicited by old and new words in episodic memory paradigms is better labeled the episodic memory effect (EM), and we will henceforth use this term.

The advent of ERP mapping studies has allowed researchers to begin to dissect the EM effect into its spatio-temporal subcomponents and determine the cognitive processes associated with each. The use of larger electrode arrays has revealed that the EM effect consists of a number of functionally different subcomponents, each with its own spatio-temporal characteristics. These different patterns of brain activity are all found primarily within a 200–1,200 ms window, although some longer-duration activity has also been found under different task demands. As will be evident from the data reviewed below, however, spatial filtering of the ERP data has revealed a variety of additional retrieval-related differences, making it clear that more spatially and temporally distinct components of the EM effect are likely to be discovered. In the following sections we review the data on each of the three major subcomponents of the EM effect in their temporal order of appearance, followed by a section on recently discovered retrieval-related activity.

Given the dichotomy between the posited familiarity and recollection processes, ERP researchers have been interested in determining which of these two processes might be reflected in the EM effect. While the EM effect was associated initially with familiarity processes (e.g., Friedman, 1990; Johnson et al., 1985; Rugg and Doyle, 1992), further research has provided compelling evidence that some aspects of it are more closely allied with recollection (Paller and Kutas, 1992; Smith, 1993; Smith and Halgren, 1989; Trott et al., 1999; Wilding and Rugg, 1996). Another line of evidence that supports this latter association is intracranial ERP data recorded from the MTL and ERP studies of patients with lesions to the MTL discussed below. Coupled with behavioral evidence that amnesics with MTL damage show greater deficits in recollection than familiarity (e.g., Aggleton and Shaw, 1996), these data strongly suggest that at least some aspects of the EM effect appear to depend on MTL structures, and therefore that these aspects reflect explicit memory processes.

To give the reader a better picture of the ERP activity discussed in the following sections, the spatio-temporal characteristics of the various aspects of retrieval-related ERP activity are illustrated using the waveforms and scalp maps from a recognition memory study by Johnson et al. (1998a). In Figure 4, the ERPs are depicted at the scalp sites where the various retrieval effects were largest, and are arranged temporally such that the earliest differences appear at the top of Figure

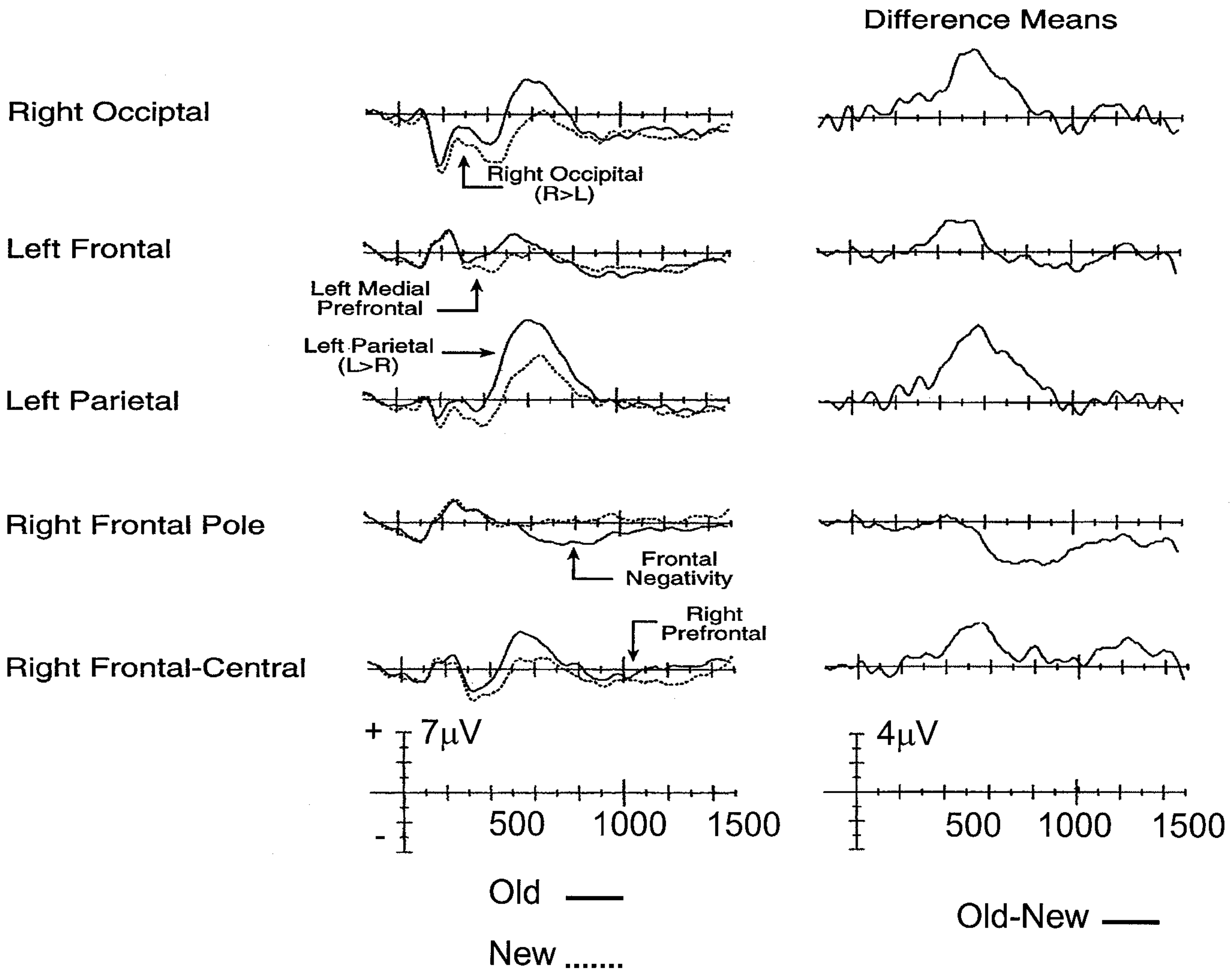

Fig. 4. Grand mean ERP waveforms elicited by correctly recognized old and correctly rejected new items from Johnson et al. (1998a). The left column depicts the old and new waveforms at the electrode site and hemiscalp where that subcomponent was largest. Repoduced from Johnson et al. (1998a) with permission of the publisher.

4. The complete pattern of brain activity is shown in the CSD maps elicited by old and new words (Fig. 5, rows 1 and 2), along with the maps of the old minus new difference waveforms (Fig. 5, row 3). For comparison with previous ERP recognition memory studies that only employed surface voltage maps, the EM differences for the surface voltages are shown in Figure 5, row 4.

Left Medial Prefrontal Subcomponent

One early sign of episodic memory retrieval appears to overlap a negative peak at 400 ms, maximal over left prefrontal-central scalp (e.g., Besson et al. 1992; Friedman, 1990; Fig. 4, row 2). Because old words elicit less negativity than new words, the old minus new subtraction makes this aspect of the episodic memory effect appear as a brief positive amplitude (Johnson et al., 1998a; Tendolkar et al., 1997). In CSD maps (row 3), it appears to be localized to left medial prefrontal scalp during the 420–590 ms epoch. In addition to this local generator activity, the pattern in the voltage maps indicates that at least part of the surface potential emanates from deep generators (Fig. 5). This early part of the EM effect is ubiquitous and some aspects of its cognitive nature have been uncovered. For example, it disappears when the lag between repeated items increases, sometime between 2 and 15 minutes (e.g., Rugg and Nagy, 1989; Smith and Guster, 1993; Van Petten et al., 1991). Using their sentence task, Trott et al. (1999) also reported that newly learned word-pair associations elicited a larger left prefrontal EM effect than did previously learned word-pair associations.

A number of lines of evidence are converging to indicate that this aspect of the EM effect indexes the familiarity process posited to contribute to recognition memory performance. For example, Smith (1993) showed that its amplitude was the same regardless of whether subjects judged the item as having been con-

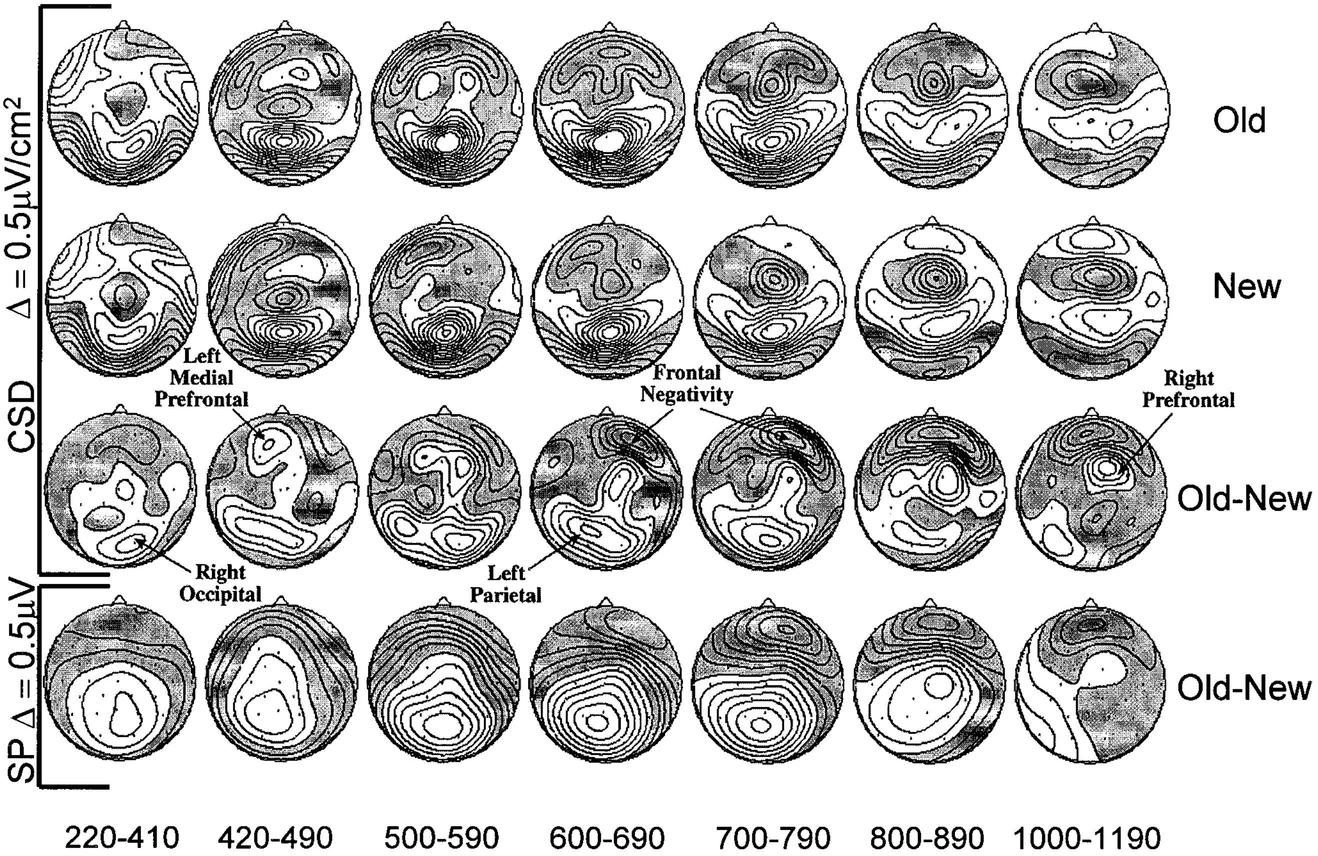

Fig. 5. **Rows 1–2:** Current source density (CSD) maps corresponding to, respectively, the old and new ERPs depicted in Figure 4. **Row 3:** CSD maps corresponding to the old-new difference ERPs depicted in Figure 4. **Row 4:** Surface voltage (SP) for the old-new difference waveforms depicted in Figure 4. Note that the large differences between the old-new CSD and SP maps (rows 3 and 4, respectively) indicate that some of the EM effect most likely emanates from subcortical structures. Reproduced from Johnson et al. (1998a) with permission of the publisher.

sciously recollected or only engendering a feeling of familiarity. Similarly, Johnson et al. (1998a) showed that neither the amplitude nor latency of this aspect of the EM effect was affected as recognition performance improved over successive study/test cycles. Although Tendolkar et al. (1997) linked this activity to associative retrieval, the fact that the apparently same activity has been found in a non-associative recognition task suggests that this left prefrontal activity is generated under a variety of recognition conditions. This conclusion has been supported by Curran (2000), who conducted an experiment based on Hintzman and Curran's (1994) plurality recognition procedure. In this experiment, subjects studied lists of singular and plural words followed by recognition tests with studied words, similar words with the opposite plurality, and completely new words. Participants were required to respond "yes" to studied words, and "no" to similar and new words. Curran (2000) demonstrated that the left prefrontal ERP activity was the same for old and similar words, supporting the idea that this aspect of the EM effect reflected familiarity. Taken together, the data strongly suggest that the left medial frontal subcomponent of the EM effect reflects a familiarity-type recognition process (Rugg et al., 1998a, had a similar result but interpreted it as an implicitly-based familiarity process). As discussed below, this left frontal activity is clearly dissociated from recollective processes that are associated with other aspects of the EM effect. Because, as mentioned above, patient data from a variety of sources support the idea that familiarity-based processes are dependent on brain areas supporting explicit retrieval, familiarity-based processes are most likely not equivalent to implicit memory. Thus, the finding that MTL lesions eliminate this early aspect of the EM effect argues that it reflects an explicitly-based memory process (Smith and Halgren, 1989).

Parietal Subcomponent

Temporally overlapping the left prefrontal positivity, an additional subcomponent of the EM effect is maximal over left parietal-occipital scalp (Fig. 4, row 3). In the CSD maps, it appears as a widespread positive current density that begins in the 420–490 ms epoch, and extends for several hundred milliseconds (Fig. 5, row 3, 420–790 ms). It is unclear, at present, whether the parietal EM effect consists of early (from about 400–500 ms) and later (from about 500–800 ms) aspects.

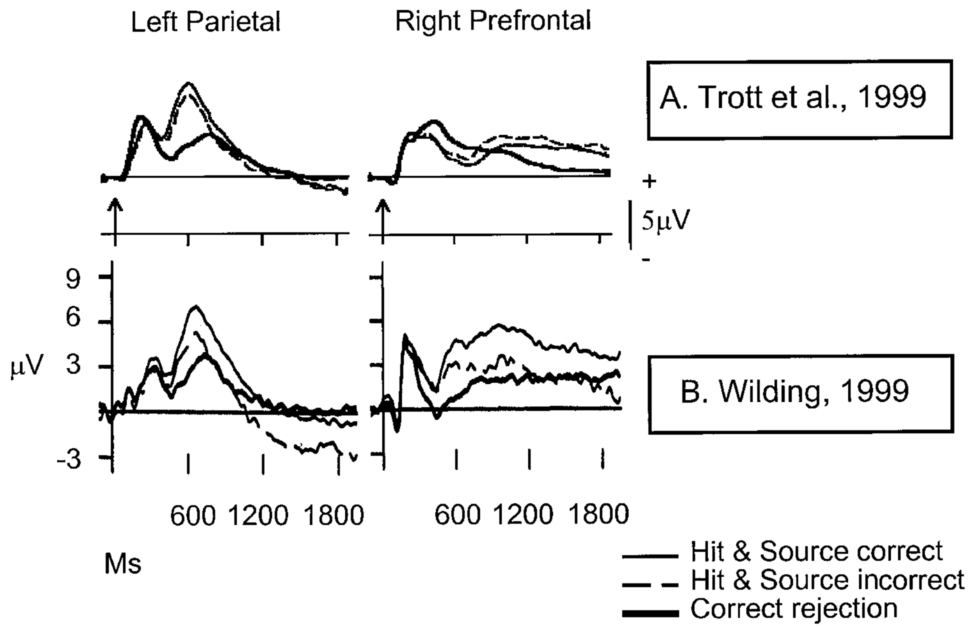

Fig. 6. ERP data recorded at left parietal and right prefrontal electrode sites from two different source memory paradigms. **A:** From Trott et al. (1999). Thick solid lines indicate the ERPs associated with correctly rejected new items; thin solid lines represent the ERPs associated with hit trials for which the list was correctly judged; dashed lines represent the ERPs associated with hit trials for which the list was incorrectly judged. **B:** Data from Wilding (1999). Thick solid lines represent the ERPs to correctly rejected new items; thin solid lines represent the ERPs to hit trials for which the gender of voice was correctly judged; dashed lines represent the ERPs to hit trials for which the gender of voice was incorrectly judged. Modified from Wilding, 1999, with permission of the publisher.

The left parietal EM effect has been the most studied, and hence much is known about its relation to episodic retrieval. Findings indicate that the amplitude of this parietal EM effect increases with study-test repetitions (Johnson et al., 1998a), is larger in association with those items rated as being consciously remembered (Smith, 1993; Smith and Guster, 1993), is larger for correctly recognized items that are subsequently recalled (Rugg et al., 1996b), and is larger for words whose study context is correctly retrieved (Trott et al., 1999; Wilding et al., 1995; Wilding and Rugg, 1996). Moreover, both old words miscategorized as new (i.e., misses) and new words miscategorized as old (i.e., false alarms) elicit parietal EM effects like those of new words (i.e., correct rejections; Johnson et al., 1998a; Smith, 1993; Wilding et al., 1995). Taken together, these data indicate that the presence of the parietal EM effect is closely allied with recollection and its amplitude is related to retrieval success.

Patient studies using the same paradigms have supported this conclusion because the left parietal EM effect was absent in patients with episodic memory deficits due to either left MTL lesions (Johnson, 1995b; Smith and Halgren, 1989) or bilateral hippocampal damage resulting from anoxia and herpes encephalitis (Johnson, 1995a). Because the ability to retrieve information about the source of an item is the foundation of episodic memory and recollection, a number of ERP investigators have included source assessment along with their recognition paradigms. While ERP activity is generally not recorded to the actual retrieval of source information, performance on the source task is used to sort trials from the recognition series to determine which aspects of the EM effect are associated with retrieval of source information. In this work, it has been assumed that ERP activity associated with correct recognition (Hits) along with a correct judgment of source is recollection-based (most likely with a contribution from familiarity as well), whereas ERP activity associated with a Hit trial for which the source has been misattributed, has been assumed to reflect a familiarity-based response.

The paradigm described by Trott et al. (1999) is a fairly typical example of an ERP source recognition memory investigation. Subjects viewed two lists of sentences in sequence (List 1 and List 2), one word at a time, in which each sentence was comprised of two unassociated nouns. Subjects were instructed to memorize the nouns and their list membership for a subsequent memory test. During recognition memory testing, all possible pairings (counterbalanced across subjects) of old and new nouns were presented sequentially, and subjects were asked to make a speeded and accurate old/new judgment to each noun. About 3 seconds after the presentation of each noun judged old (regardless of its study status), subjects were prompted to indicate both whether their recognition was based on recollection ("remember") or familiarity ("know") and from which list the noun had come. Temporal order (first or second list) thus served as the critical contextual feature for each noun. In this way, Trott et al. (1999) attempted to objectify the fairly subjective judgments of remember and know.

The ERP waveforms and scalp distributions are depicted, respectively, in Figures 6 and 7 from two source memory studies. The data in Figure 6 are sorted according to whether the correctly recognized old item was associated with a correct (hit and source correct) or incorrect (hit and source incorrect) judgment of source. The ERPs to new items are shown for comparison. As can be observed from inspection of Figures 6 and 7, there is a high degree of similarity among the waveforms and scalp distributions across studies (Trott et al., 1999; Wilding, 1999), despite the fact that each employed a different contextual feature to define source. In Trott et al. (1999), it was list membership (List 1 or List 2), while in Wilding (1999) it was the gender of the voice in which the word was spoken

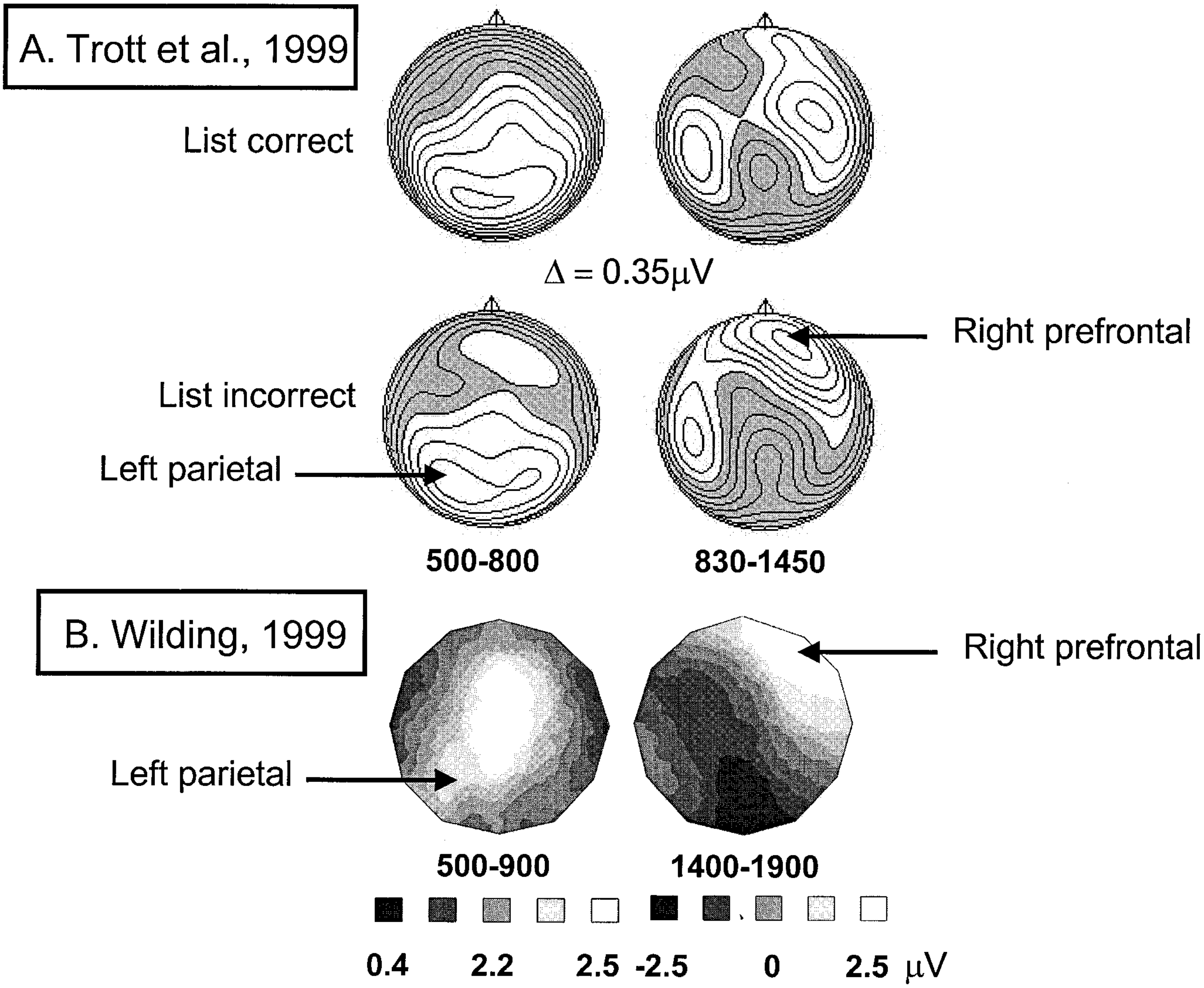

Fig. 7. Scalp distributions of the ERP EM effects depicted in Figure 5. **A:** Data from Trott et al. (1999) for hits associated with list correct and incorrect judgments. The isopotential lines are separated by 0.40 microvolts. **B:** Hits that attracted correct gender of voice judgments. Reproduced from Wilding, 1999, with permission of the publisher.

during study. When the subject correctly recognized an old item and also correctly identified its source, the left parietal EM effect was larger than when the source was incorrectly identified. (Although the amplitude difference in Fig. 6 for the positive peak at 600 ms over the left parietal site is larger in Wilding's data, Trott et al.'s difference was statistically reliable). Moreover, both these waveforms were larger than the ERPs to the corresponding new items, indicating robust EM effects for the ERPs associated with each of these two behavioral outcomes.

As discussed above, many memory theorists posit that recollection and familiarity are unique states of awareness with distinct neuroanatomical underpinnings. It follows, therefore, that there should be differential patterns of brain activity associated with each type of retrieval (e.g., Duzel et al., 1997; Gardiner and Java, 1990; Squire, 1994). However, as is evident from the top two rows of Figure 7, the scalp distribution of the left parietal EM effect (500–800 ms) associated with Hit trials whose source was correctly attributed cannot be differentiated from the scalp distribution of a Hit trial associated with an incorrect source judgment (Trott et al., 1999; scalp distribution data for the source incorrect waveforms were not available from the Wilding, 1999, study).

Another method for assessing possible differences between recollection and familiarity is with the Remember/Know procedure. In addition to using the Remember/Know procedure to study acquisition differences, ERP researchers have used this procedure to determine if there are neural differences associated with these states of awareness during retrieval (Duzel et al., 1997; Rugg et al., 1998b; Trott et al., 1999). Trott and colleagues (1999) found a larger parietal EM effect to items that were correctly recognized and given a remember judgment compared to that associated with correct recognition and given a know judgment. Importantly, neither of these EM effects could be distinguished on the basis of scalp distribution. Amplitude differences in the absence of distributional differences indicate that, although the same brain areas were active for both judged categories, there was more activity for the recollected items. Such results suggest that it is likely that these two behavioral outcomes reflect a graded continuum, in which some contextual information is available, but not sufficient to allow full integration of the item with its initial learning context. Note that the Trott et al. (1999) distribution results contradict the distributional data and conclusions of Duzel and co-workers (1997). Based on their visual observation that the scalp distributions of the parietal portion of the EM effect associated with remember and know judgments appeared to be different, Duzel et al. interpreted this result as indicating that there are cognitively and neuroanatomically distinct states of awareness associated with these two judgments. Unfortunately, these results are equivocal because Duzel and colleagues (1997) did not normalize their amplitude data, and thus cannot rule out the possibility that their effects were due to amplitude differences rather than differences in scalp topography (see Ruchkin et al., 1999, for a discussion of this point). In the only other study using the Remember/Know technique that also evaluated normalized scalp distribution data, Rugg and colleagues (1998b) did not have enough artifact-free trials to calculate ERPs for Know judgments and thus could not comment on possible differences as a function of type of retrieval judgment. However, an examination of figure 5 in Rugg et al. (1998b) shows that their left parietal scalp distribution of the ERPs associated with remember judgments was highly similar to that reported by Trott et al. (1999). It thus appears that the nature of the differences between the parietal EM effects associated with remember and know judgments is still unresolved.

Given that the left and right hippocampal formations appear to support memory for verbal and spatial memories, respectively, ERP investigators have looked for and found material-specific asymmetries in the parietal EM effect. In one such study, Mecklinger (1998) had subjects perform both object form and spatial location recognition memory tasks in an attempt to better define the functions of the parietal EM effect. Subjects were cued at test, randomly by trial, about which recognition task to perform. While the object and spatial parietal EM effects occurred at similar times (approximately 500 ms to peak), the results showed that the scalp distribution of the parietal EM effect varied as a function of the type of material that was retrieved, being right centro-frontal in the object task and bilaterally symmetric over occipital scalp during spatial location retrieval trials. Mecklinger's (1998) results, in combination with those of previous studies showing a left posterior focus for verbal stimuli, suggest that there are multiple parietal aspects of the EM effect that are material specific. Future studies will determine if these material-specific results hold for different kinds of stimulus materials when correct and incorrect source judgments are considered.

Right Prefrontal Subcomponent

A third subcomponent of the EM effect, maximal over right central-frontal scalp, begins between 500–590 ms and may last until the end of the recording epoch (Fig. 4, bottom row; e.g., Allan et al., 1996; Allan and Rugg, 1997; Johnson, 1995a; Trott et al., 1999; Wilding and Rugg, 1996, 1997). As shown in the CSD maps (Fig. 5, row 3, 500–1,200 ms), the timing of this right prefrontal subcomponent is such that, although it typically begins soon after the left parietal EM effect, its duration exceeds the posterior activity by several hundred ms. At present, a consensus on the functional role of the right prefrontal subcomponent is still lacking.

Given that the frontal lobes play a major role in the retrieval of source information, this aspect of episodic memory seemed a likely candidate for the cognitive process underlying the right frontal EM effect. Although a number of ERP researchers have investigated the relation between the right prefrontal activity and source memory, they have met with mixed success. Based on their early studies, Wilding and Rugg (1996, 1997) suggested that the right prefrontal scalp activity might reflect the *successful* retrieval of source information, as they found that this activity was larger when the source was correctly identified (see Fig. 6B). They suggested further that this effect might be dependent upon a mechanism located in right prefrontal cortex, consistent with the PET and fMRI studies demonstrating right prefrontal activation during memory retrieval. On the other hand, as is evident in the Trott et al. waveforms (Fig. 6), right prefrontal activity was greater when source retrieval was *unsuccessful*. Furthermore, Trott et al. (1999) observed that the same activity was elicited by false alarms (new items called old) during recognition testing, items that could not have been retrieved from memory. Trott et al. (1999) concluded, therefore, that this activity reflected post-decisional aspects of mnemonic processing, and was not contingent upon successful retrieval of contextual information. Similarly, Ranganath and Paller (1999a) recorded this right prefrontal activity in an old/new recognition test, but not in a task requiring retrieval of specific information about a picture's original orientation during study. Taken together, the data suggest that the right prefrontal EM effect does not reflect retrieval success for the item's initial learning context.

One problem in interpreting the functional significance of the right prefrontal EM effect is its extended temporal course, from approximately 500–2,000 ms. Because this extended ERP component fits with the presumed long durations of the cognitive processes underlying this activity (e.g., retrieval of contextual information; operating on the products of retrieval), investigators have tended to measure it over long temporal intervals. This practice may contribute to the lack of comparability across studies. That is, without quantifying this activity over shorter intervals, it is not possible to determine if the right prefrontal activity reflects one long, continuous pattern of brain activity, or multiple subcomponents of the EM effect occurring within shorter time spans. Alternatively, if the right prefrontal activity were linked to a process such as operating on retrieved information, then the onset and duration of this retrieval processing would be highly dependent both upon the nature of the stimuli and the nature of the task. In either case, it is necessary to map the right prefrontal activity over shorter intervals to determine which of these two patterns obtains.

Further complicating efforts to characterize this aspect of the EM effect, a number of investigators have found a slow positivity appearing in the 1,200–1,990 ms post-decisional epoch, after the offset of the left parietal EM effect. Like the right prefrontal EM effect, this activity was maximal over right central-frontal scalp, but unlike that effect, was present to *both* correctly rejected new and correctly recognized old items (Allan and Rugg, 1997; Johnson et al., 1998a; Rugg et al., 1996; Tendolkar et al., 1997; Wilding et al., 1995). While the role of this post-decisional right prefrontal positivity is unclear, a number of investigators have concluded that, because of its presence to new items, it is not necessary for episodic retrieval (Johnson et al., 1998a; Tendolkar et al., 1997).

Another methodological feature that must be taken into account is the fact that attempts at interpreting the right prefrontal EM effect have resulted from source memory paradigms in which the source judgment occurred some few seconds *after* the initial old/new judgment had been made. This second decision occurred during a period when ERP activity was not recorded or averaged. The sequential nature of the two judgments may have forced participants to adopt a serial processing strategy, in which an old/new judgment was initially made, followed by a search for and retrieval of source information. In such a situation, brain electrical activity related to retrieval of context may not have been recorded during the interval when source recollection had actually taken place. However, arguing against this possibility are data reported by Senkfor and Van Petten (1998), who asked their participants to make old/new recognition and source (gender of voice) judgments in separate blocks of trials (in the latter case, subjects made a 3-choice response: same voice; different voice; new). Common to both recognition and source blocks were a parietal EM effect and a later-onsetting right prefrontal EM effect that was larger in the source recognition task. Hence, even though Senkfor and Van Petten (1998) required source judgments at the time the ERPs were recorded, the ERP data indicated that an old/new decision was generated first, followed by a search for source information. Nonetheless, it could still be argued that the nature of the response requirements in the source task (old same source; old different source; new source) required subjects to adopt a strategy in which an old/new decision was made earlier than the retrieval of contextual information. To counter this argument, Senkfor and Van Petten (1998) constructed a second experimental series in which recognition was followed by a source decision task during which no new items occurred. Comparison of the ERPs associated with correctly identified source trials with the ERPs elicited by correctly rejected new items and correctly recognized old items during the recognition task revealed that the right prefrontal positivity was prolonged relative to the parietal EM effect even though an old/new judgment was not specifically required.

Evidence that the right prefrontal EM effect might reflect post-retrieval monitoring operations has recently been provided by Wilding (1999) who manipulated the kinds of source information that had to be retrieved. At study, subjects heard words presented in either male or female voice and made an active/passive judgment or a pleasant/unpleasant judgment. In one retrieval test, subjects had to retrieve the gender of the voice in which the word had been spoken at study, while in another, they attempted to retrieve the kind of task (action or liking) they had performed on the given word during the study phase. The results revealed larger right prefrontal effects in the retrieval of task compared to the retrieval of voice condition. Importantly, this difference also obtained for the ERPs elicited by correctly rejected new items. As these items had not been seen during study, no episodic mnemonic information could have been retrieved. Wilding (1999) concluded that the right prefrontal EM effect could not have reflected retrieval success, suggesting instead that it reflected processes that “monitor for certain kinds of retrieved information” (Wilding, 1996, p 451).

Further evidence against the idea that the right prefrontal EM effect reflects successful retrieval has been provided by Ranganath and Paller (1999b). These investigators employed a different approach, in which highly distracting environmental sounds were delivered while subjects retrieved either autobiographical or semantic memories. Based on neuropsychological (e.g., Knight, 1984) and experimental (e.g., Fabiani and Friedman, 1995; Friedman et al., 1999) evidence, the ERP response to novelty, the “novelty P3,” is thought to depend upon intact frontal cortex. Hence, Ranganath and Paller (1999) predicted that the novelty P3 would be reduced in amplitude to the extent that novelty detection and memory retrieval interfere with one another. In line with their prediction, novelty P3 amplitude was reduced over right prefrontal scalp sites during episodic retrieval, whereas a similar but less lateralized pattern was obtained during semantic retrieval. This was not the case during a control, tone counting condition. Although not clarifying the role that these frontal activations might play during retrieval, these data are important because they demonstrate that right prefrontal activations may occur not only during episodic retrieval but also during semantic retrieval. One possibility is that the reduction in novelty P3 amplitude observed by Ranganath and Paller (1999b) has more to do with the strategic aspects of memory retrieval, than it does with a mnemonic function per se. Nevertheless, consistent with other studies, these data suggest that the right prefrontal EM effect does not reflect retrieval success of the original study context.

Further complicating the assignment of a uniform functional role for the right prefrontal EM effect are recent data demonstrating material-specific topographies for this activity. Mecklinger’s (1998) study of object and spatial memory described above also revealed a right-lateralized ERP component beginning around 1,200 ms that, like the left parietal EM effect, had a material-specific topography. This activity was frontally focused and right lateralized during object form trials (perhaps synonymous with the right prefrontal activity described above) and bilaterally symmetric and focused around central scalp during spatial location trials. Such findings are difficult to reconcile with previously advanced putative functional roles of the right prefrontal EM effect as no similar variations in scalp topography have been reported.

In summary, the recently revealed multi-component nature of the EM effect fits well with dual-process theories of recognition memory based upon behavioral data. Using different approaches, it appears that different temporo-spatial patterns of brain activity underlie the familiarity and recollection processes posited in dual process models of recognition. These ERP studies have shown that the left medial prefrontal EM effect, which has been associated with familiarity, begins about 100 ms earlier than the left parietal EM effect, which varies in a manner consistent with the idea that it reflects recollective processes. Studies of patients with MTL lesions showing that both of these EM effects are reduced or absent lend support to the conceptualization that both familiarity and recollection are explicit memory processes. Although present consistently across a wide variety of retrieval tasks, the exact nature of the processes underlying the right prefrontal subcomponent of the EM effect remains unclear at present.

OTHER RECOGNITION-RELATED ACTIVITY

In the first CSD analysis of an old/new recognition task, Johnson et al. (1998a) found a number of additional memory-related ERP components. One, an earlier EM effect than has been reported previously, is evident as a greater negativity for new than old words over right occipital scalp in the 220 to 410 ms interval (Fig. 4, row 1). The CSD maps of the old/new difference show this as an area of positive current density localized to a scalp region overlying right occipital cortex (Fig. 5, row 3). Given its location over early visual processing areas and the fact that there was more neural activity for unexperienced items, this brain activity is consistent with the areas activated in hemodynamic studies of perceptual priming (e.g., Squire et al., 1992).

Another new pattern of brain activity, apparent over far-frontal scalp, begins about 200 ms post-stimulus and continues until about 1,400 ms (Fig. 4, row 4). Further, it appears to be comprised of two, and possibly three, distinct subcomponents. As shown in the CSD maps, the first putative subcomponent, which is larger over the left frontal pole and active between 400–690 ms, is similar in magnitude in both old and new ERPs (see Fig. 5, third and fourth columns, top two rows of maps). Like the parietal EM effect, the early, far-frontal negative current density between 500 and 590 ms tended to be larger as recognition performance improved but, unlike the parietal EM effect, the same amount of activity was elicited by old and new words (Johnson et al., 1998a). The very early onset of this far-frontal negativity, coupled with its elicitation by both old and new words, raises the possibility that it represents processes that may organize or guide attempts to retrieve information from episodic memory, functions known to depend on the frontal lobes (e.g., Moscovitch, 1992). Consistent with this idea, the magnitude and duration of this negativity was similar when the same subjects performed an episodic cued recall task (i.e., using the first three letters of the same words as cues; Johnson et al., 1998b). In addition, early, bilateral negativities with the same duration, but twice the amplitude, were elicited in a task requiring retrieval of source information about these same words (Johnson, unpublished observations). Further evidence that this negativity appears to be related specifically to episodic retrieval comes from the fact that it was not elicited when the same subjects performed a semantic cued recall task (Johnson et al., 1998b).

A second subcomponent of this far-frontal activity occurs between about 600 to 790 ms and is maximal over the right frontal pole (Fig. 4, row 4). In contrast to the left frontal pole activity, right frontal pole activity is larger in the ERPs elicited by old compared to new words (Fig. 5; third row of maps, fourth and fifth columns). The timing of this activity suggests that it was related to the retrieval of episodic information, perhaps monitoring the retrieved episode. A third possible subcomponent is evident as a shift in the negative current density from the right frontal pole to a more symmetrical distribution (Fig. 5, right two columns, third row). This shift, which begins around 800 ms and continues at least until 1,200 ms, is again only present in response to the old words. Its post-retrieval timing suggests that it may reflect brain activity related to utilization of the retrieved information to guide behavior.

Yet another frontal aspect of the EM effect or a task-specific variation on the right prefrontal subcomponent was reported by Donaldson and Rugg (1999). This activity was bilateral, and frontally-distributed and temporally intermediate between the left parietal and right prefrontal subcomponents (Donaldson and Rugg, 1998, 1999; Wilding and Rugg, 1997). In the Donaldson and Rugg (1999) investigation, subjects studied lists of paired and previously un-associated words, and then immediately performed in either associative recognition or associative recall tasks, with subjects cued randomly by trial about which information to retrieve. On the recognition trials, subjects had to decide whether a pair of words was old or new and, for pairs judged old, whether they were presented in the same order or rearranged. For associative recognition, Donaldson and Rugg (1999) only analyzed the ERPs associated with correctly identified new pairs and recognized old pairs that had been correctly judged "same." During associative recognition, the ERPs elicited by correctly recognized old "same" showed a left parietal (600–900 ms), and a right frontal (1,400–1,900 ms) EM effect. In addition, they reported a bilaterally-symmetric, frontal ERP component, between 900 and 1,400 ms, whose functional significance remains unclear. Nevertheless, the presence of the left parietal and right prefrontal EM effects in associative recognition suggests that these activities reflect mnemonic processes that are common to a broad range of memory tasks.

When subjects have multiple opportunities to study the same items, performance improves (i.e., faster RTs and higher recognition rates). To determine how such performance changes affect brain activity, Johnson et al. (1998a) attempted to identify repetition-related differences in ERP activity during a recognition memory task (across four study/test phases). When the perfor-

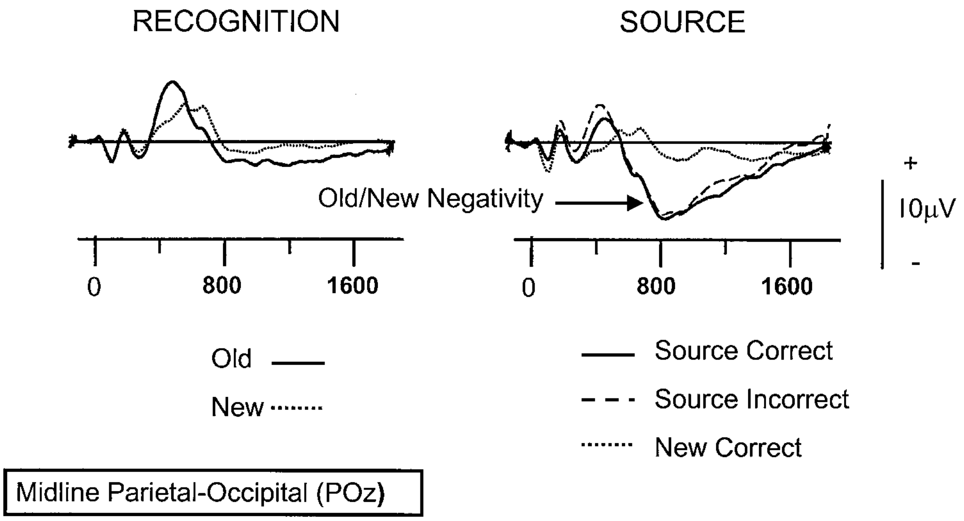

Fig. 8. Grand mean ERPs elicited during recognition (**left**) and source (**right**) recognition memory tasks. Left: Waveforms associated with correct recognition judgments. Right: ERPs associated with correct and incorrect "source" judgments. POz = midline parietal-occipital electrode site.

mance-related amplitude increases were isolated by subtracting the old and new ERPs at Test 1 from those elicited at Test 4 (i.e., Old4 minus Old1), a pattern of brain activity that was temporally and spatially distinct form the EM effect was found. This difference was maximal between the midline central and parietal sites, anterior and medial to the parietal EM effect. Extending from 500 to 900 ms, the repetition-related positivity was also temporally dissociable from the parietal, and left and right frontal subcomponents of the EM effect. As Johnson et al. (1985, 1998a) noted, this ERP activity cannot be a direct representation of memory trace strength because the magnitude and scalp distribution of this repetition-related activity was the same for *both* old and unrepeated new words. Thus, although the ability to discriminate old from new must be based on some trace strength-related measure, it is equally plausible that the repetition-related positivity reflects cognitive processes associated with decision confidence. Therefore, whether the repetition-related positivity reflects decision confidence, or other processes dependent on trace strength or discriminability, it is clear that this activity occurs in brain circuits separate from the other main aspects of the EM effect.

Memory retrieval has been conceptualized as involving the reactivation of neural ensembles that were initially utilized to encode the episode. In accord with this principle, Cycowicz et al. (unpublished observations) have shown ERP evidence of the activation of sensory cortical regions during retrieval that reflect the processing active during encoding. During study, participants viewed line drawings of common objects outlined in either red or green, and memorized the objects and their associated colors for subsequent memory tests. As shown in Figure 8, an old/new negativity is present only when the perceptual attribute (color) has to be retrieved (between about 800–1,000 ms). Figure 9 depicts the distributions of the old-new difference ERPs associated with this late negative source retrieval effect. In contrast to what would be predicted by the conceptualization described above, the occipital, sensory activity was not present when subjects simply had to make an old/new decision. Rather, the occipital activity was elicited only when subjects were required to retrieve information about the perceptual source of the memory. This negative activity could reflect a material-specific search for source (i.e., color) information (see also Johnson et al., 1996).

To summarize, as the range of variables has increased in studies employing larger arrays of electrodes there has been a concomitant proliferation of memory-related ERP components. While some of these new components fall into the category of EM effects, others appear to span the full range of retrieval-related processes such as priming, strategic processes engendered by both old and new items, monitoring and utilization of retrieved information, decision confidence, and retrieval of source information. Nevertheless, the links between these various ERP components and each of these cognitive processes need to be strengthened in future studies.

ERP Results: Recall

While recognition-related processes have been well studied by ERP researchers, the equally important processes underlying cued and associative recall have received considerably less attention. Given that these are two routes by which the same information can be accessed, how the neural processes underlying each differ is of considerable interest. To date, only three recent reports have described recall-related ERP activity, all of which used a word-stem cued recall paradigm (Allan et al., 1996; Allan and Rugg, 1997; Johnson et al., 1998b). Allan et al. (1996) reported that the sole ERP effect was a long-lasting (i.e., 300–1,400 ms) positive shift, maximal over frontal scalp, that was elicited during episodic retrieval relative to semantic retrieval. However, as pointed out by Johnson et al. (1998b), there are methodological concerns that undermine Allan and Rugg's (1997) interpretation that EM effects are dependent on retrieval task. This is because their experimental design required subjects to perform two sequential tasks during semantic stem cued recall, but only one during the episodic recall and recognition trials.

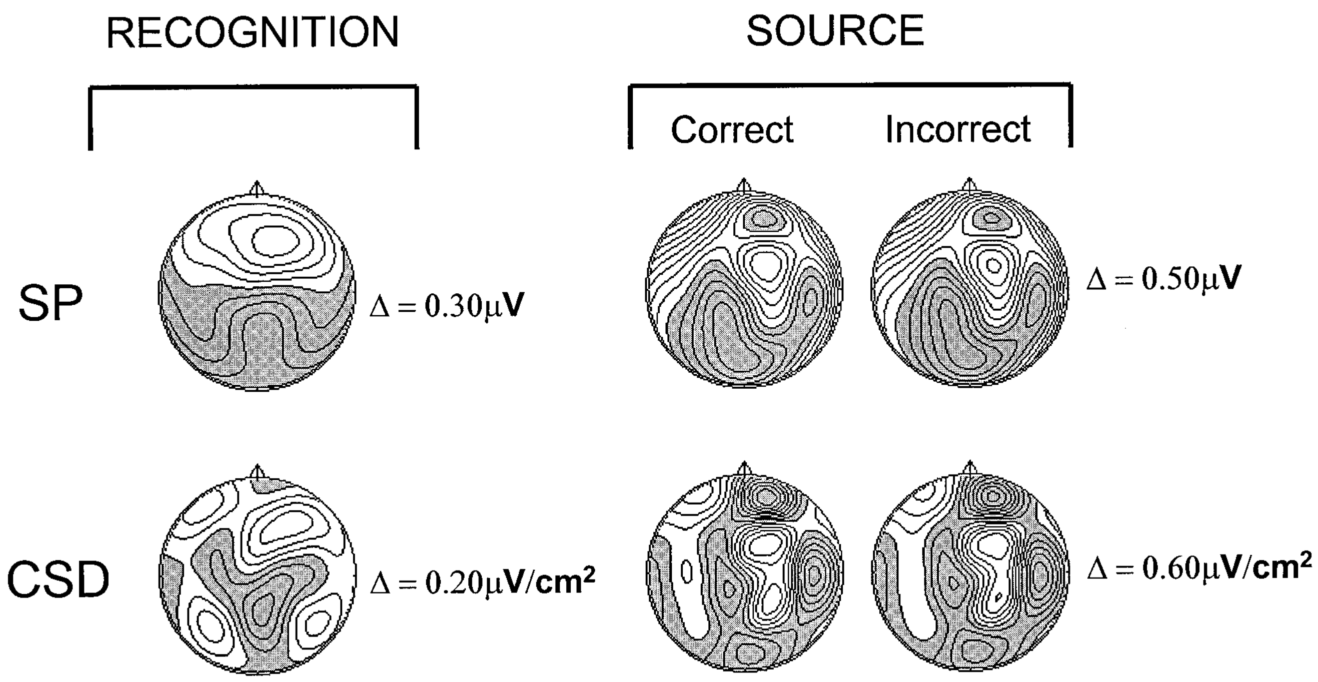

Fig. 9. Surface potential (SP; **top**) and current source density (CSD; **bottom**) maps based on the difference waveforms. The difference ERPs were obtained by subtracting the ERPs associated with correctly rejected new pictures (recognition and source; different new items for each) from the ERPs elicited by pictures associated with correct old (recognition) and correct and incorrect (source) decisions based on the ERPs depicted in Figure 8. The maps are depicted for the old/new negativity labeled in Figure 8.

To counteract this problem, Johnson and co-workers (1998b) had subjects study two lists of words. One list was memorized at home ("Home List") prior to the recording session. Subjects were only admitted into the study if, after 1 week, they could freely recall 90% of the 80 words on the list. During the experimental session, subjects learned a second list in a series of study-test blocks ("Lab List"). Episodic recall for the Home and Lab lists was compared with semantic recall (i.e., completing the stems with the first word that came to mind). The three lists were constructed such that they were comprised of mutually exclusive groups of stems so that there was no overlap in the completions that could be provided in response to the stems of the three lists. With this design, Johnson et al. (1998b) could assess brain activity differences as a function of memory system (episodic vs. semantic), retrieval task (recall vs. recognition), and retrieval difficulty (Home vs. Lab lists). As shown in the CSD maps in Figure 10, both semantic and episodic recall were characterized by activity localized over left inferior prefrontal, central, temporal, parietal, and inferior posterior scalp in the 500 to 900 ms epoch. However, episodic recall was distinguished from semantic recall by greater negative activity over the frontal poles and right prefrontal areas. This right frontal negative activity began 100–200 ms prior to the subjects' responses signaling successful recall for the episodic conditions but after the response in the semantic condition. Johnson et al. (1998b) interpreted these results as suggesting that subjects use the left inferior frontal area for generation of possible completions during both the episodic and semantic recall tasks. Further, given its timing, it was suggested that the right frontal pole activity might reflect the additional processes that would be necessary during episodic recall to select the correct response from all generated possible endings (e.g., monitoring). That this right frontal pole activity was the same when subjects recalled the Home and Lab list words, despite the large differences in percent recall, is consistent with the idea that it reflects processes related to retrieval success rather than to those related to retrieval effort.

While there are still relatively few data, it is possible to address the question of how brain activity differs as a function of retrieval task (i.e., recognition vs. recall). For example, in a follow-up to Allan et al. (1996), Allan and Rugg (1997) replicated their earlier recall finding and showed that the distribution of the sustained frontal positivity elicited during the cued recall task was different from the right prefrontal EM effect elicited during recognition. The authors, therefore, concluded that these different patterns of brain activity present during recall and recognition reflected the operation of common explicit retrieval mechanisms that differed according to the type of cue (whole word or stem) presented at test. The results from Allan and co-workers are significant because they suggest that the ERP activity elicited during episodic memory tasks is dependent on retrieval task.

As indicated above, the Johnson et al. (1998b) study of recognition also included a recognition series for comparison. The bottom two rows of Figure 10 show the CSD maps for the same old words when they were retrieved via the word-stem cues or recognized (bottom row). Note that the mapped epochs are different for recall and recognition due to differences in retrieval

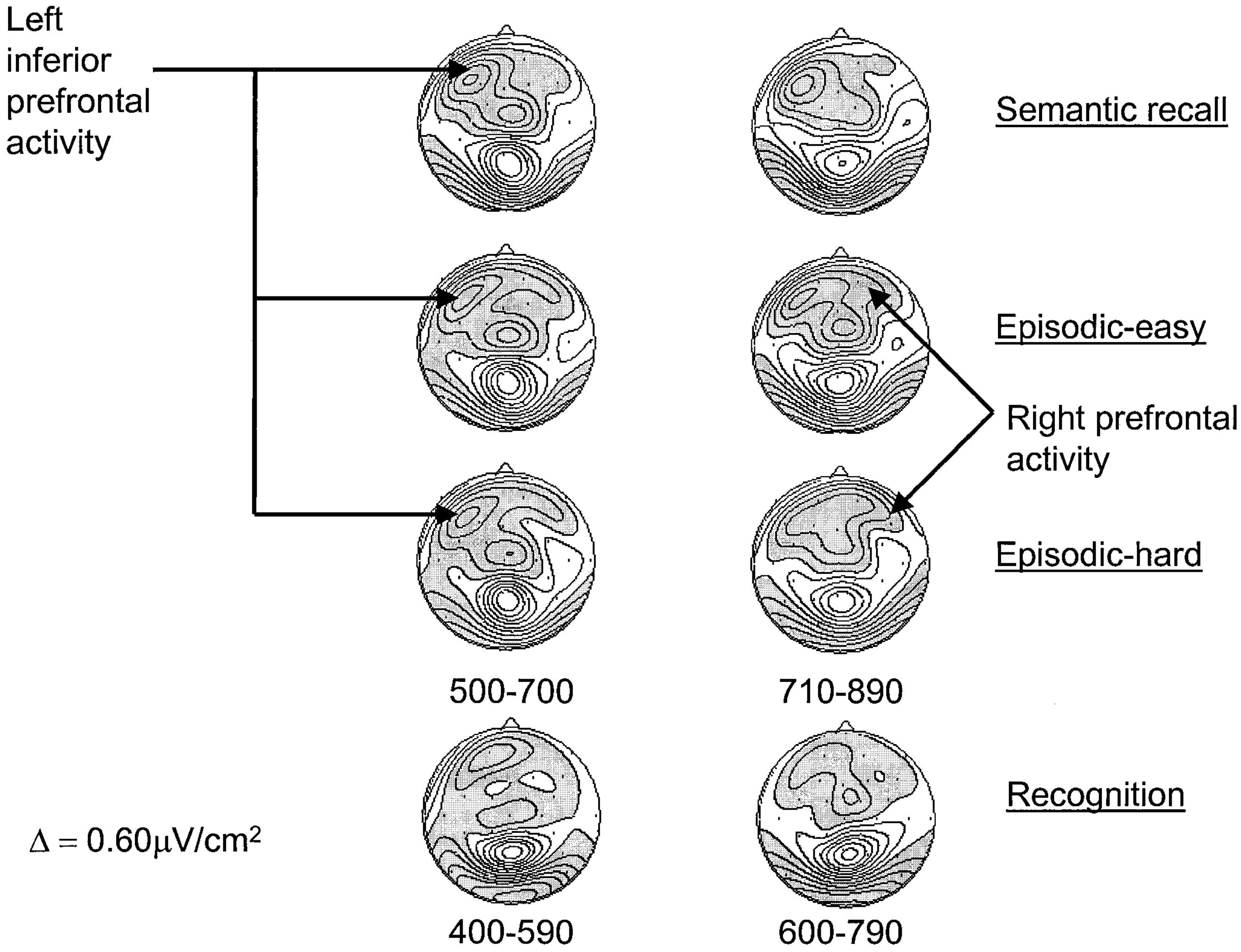

Fig. 10. Current source density maps of ERP activity during semantic (**top row**), episodic easy (home list; **second row**), episodic hard (Lab list; **third row**), and recognition (**bottom row**) retrieval conditions. Isopotential lines are separated by 0.60 μV/cm^2. Modified from Johnson et al. (1998a, 1998b) with permission of the publisher.

timing. These maps reveal that both episodic recall and recognition elicited similar patterns of brain activity over far frontal, central, temporal, parietal, and inferior posterior scalp. However, the left inferior prefrontal activity elicited during recall was largely absent during recognition. In addition, the typical left parietal EM effect was masked during episodic recall (i.e., episodic minus semantic) due to the large differences in the variability of retrieval timing that occurred between episodic and semantic recall. When the variations in retrieval timing are eliminated from the recognition and recall conditions via response-synchronized averaging, at least the parietal and right frontal EM effects appear to be the same regardless of retrieval task (Johnson, unpublished observations). Similar results were obtained using an associative recall task, when Donaldson and Rugg (1999) reported that the left parietal EM effect found during recall (i.e., semantic vs. episodic recall) was very similar to that observed during recognition.

In summary, although there are still only a few studies, the recall data provide a strong association between at least the left parietal and right frontal EM effects and recollection and highlight the fact that overlapping brain networks are activated during different types of episodic retrieval. An important difference between word stem cued recall and recognition is the presence of left inferior prefrontal activity in the former, presumably because subjects need to generate possible completions for the word stems during cued recall.

ERP Intracranial and Brain Injury Studies

While it is difficult to infer the brain generator sources of scalp-recorded ERP data, such information is available from patients with implanted intracranial electrodes. Although there are some difficulties linking intracranial potentials with specific scalp-recorded ERPs (for a discussion see Halgren et al., 1998), episodic memory potentials have been recorded in and around the temporal lobes. For example, using a continuous recognition task, Smith et al. (1986) showed that (1) intracranial ERPs were comprised of enhanced positivity or reduced negativity to the previously studied word as were their presumed scalp homologs (between about 300–800 ms); and (2) these episodic memory potentials had generators within several MTL structures, including the hippocampus, parahippocampal gyrus, and amygdala. Since this initial finding, a few other teams have replicated this basic phenomenon (e.g., Elger et al., 1997; Grunwald et al., 1999; Guillem et al., 1995). Thus, the extant data suggest that these MTL structures probably contribute to the parietal EM effect recorded at the scalp.

Further evidence consistent with an MTL contribution to the EM effect comes from scalp-recorded ERP data in post-surgical epilepsy patients who have undergone either right or left temporal lobectomy (RTL or LTL) (e.g., Johnson, 1995b; Rugg et al., 1991; Smith and Halgren, 1989). Smith and Halgren (1989) observed a dramatic reduction of the parietal EM effect in LTL patients compared to controls and RTL patients during a word recognition memory paradigm. The LTL patients showed mild behavioral deficits in recognition memory, which suggested to Smith and Halgren (1989) that the patients must have based their decisions on familiarity. Therefore, Smith and Halgren (1989) interpreted the parietal EM effect as reflecting the recollective component of recognition memory and suggested that familiarity did not modulate this aspect of the EM effect. In another study of temporal lobectomy patients, Johnson (1995b) replicated Smith and Halgren's (1989) behavioral and ERP results by showing that overall lower levels of correctly recognized old words in the LTL patients was accompanied by the lack of the parietal EM effect. The RTL patients, in contrast, had performance and episodic ERP effects that were comparable with those of the controls. Moreover, having used repeated lists, Johnson (1995b) extended the Smith and Halgren results by showing that the learning demonstrated by the LTL patients over successive tests was associated with the same increases in the central-parietal repetition component (see above) observed in the controls and RTL patients. These data suggest that the changes in strength/accessibility of the memory trace that occur as a result of practice were unimpaired in the LTL patients, despite lowered overall recognition performance. In addition, because a recall test revealed greatly impaired performance in the LTL patients relative to the controls and RTL patients, these data support Smith and Halgren's conclusion that the parietal EM effect reflects recollection, rather than familiarity. A further sign of the limited nature of the LTL patients' memory deficit was the fact that their right prefrontal EM effect appeared to be intact. Similarly, Johnson (1995a) reported that severely amnesic patients, who were unable to make any new episodic memories, did not show the parietal EM effect or any strength effect on the LPC in accord with their chance recognition performance across repeated study-test cycles. Additional, confirming evidence comes from a study by Mecklinger and colleagues (1998), who reported that the left parietal EM effect was absent in patients with memory loss due to transient global ischemia. All of these patient data argue for the idea that at least the left parietal EM effect reflects a recollective-type retrieval process.

Intracranial recordings have also been obtained from frontal lobe structures in these same pre-surgical epilepsy patients (e.g., Guillem et al., 1995, 1996), although only in yes/no recognition tasks. Although a right prefrontal EM effect might not be expected in such simple memory tasks, Guillem et al. (1995) did observe large-amplitude early EM effects in their frontal electrodes, and suggested that this intracranial activity probably contributed to the left frontal activity recorded at the scalp.

In sum, the results of these studies suggest that at least some of the scalp-recorded ERP memory components discussed here have homologs in the intracranial data. Moreover, this MTL generator activity, most likely in combination with other subcortical structures, is likely responsible for the apparently large amount of subcortical activity evident from the differences between CSD and SP maps (see Fig. 5; the differences between rows 3 and 4)

Integration of Retrieval ERP and Hemodynamic Results

Overall, there appears to be a good degree of concordance between the locations of the retrieval-related scalp ERP activity and those revealed by PET and fMRI techniques. Although the different brain imaging techniques provide different types of information concerning brain activation, the relation between the experimental variables and magnitude of ERP and hemodynamic indices appear to be converging on similar functional interpretations. In addition, to the degree that the concordance between ERP and hemodynamic data can be established, the ERP data provide information on the sequencing and duration of these activations. With the caveat that the proposed pairings of ERP and fMRI/PET results remain speculative, the attempt to combine the temporal information inherent in the ERP with the spatial information available from fMRI/PET is, nevertheless, an instructive exercise.

The earliest ERP distinction between old and new items (between about 200–400 ms) appears to be a right occipital potential that is *smaller* for previously studied words (Figs. 4 and 5; see also Paller and Kutas, 1992), in highly similar fashion to blood flow deactivation in right occipital cortex recorded during word stem completion (Squire et al., 1992). These data suggest that the reduced activity observed in both the ERP and hemodynamic data is a correlate of priming, i.e., the brain does less neural processing in response to a repeated stimulus with which it is "fluent." Immediately following this response, a positivity that is larger for old items is elicited over left medial prefrontal scalp between about 400 and 500 ms. It is presently unclear if this ERP subcomponent has a homolog in the hemodynamic data. The left parietal EM effect, spanning the 400 to 800 ms interval, appears to reflect the recovery of episodic information. CSD maps suggest the presence of generators that correspond well with the commonly observed precuneus (Brodmann Area [BA] 19) activations in hemodynamic studies (e.g., Henson et al., 1998). However, differences between surface voltage and CSD mapping studies suggest that this cortical aspect is only part of the response and that there must be additional generators in subcortical areas. Studies of patients with localized lesions and/or intracranial electrodes suggest that the deep generators of this electrical activity may reside in the MTL, and these putative generator sites would fit well with hippocampal activations that have been observed in a number of blood flow studies of retrieval (e.g., Schacter and Wagner, 1999).

ERP activity is also seen over frontal and far frontal scalp, with additional and/or larger potentials over the right than left hemisphere. The high degree of variability in frontal results across studies suggests that there are a number of different patterns of activity in the 500 to 2,000 ms interval. Some of those elicited exclusively by old items undoubtedly reflect retrieval of the item itself, its source, or the use of the retrieved information. Still other frontal ERP components appear to reflect more strategic aspects of retrieval that are state related because, although they are elicited by both old and new items, they are elicited during episodic but not semantic retrieval tasks. The varied results of ERP studies with respect to frontal activity are paralleled in the results of blood flow studies. Nevertheless, recent blood flow studies by Buckner et al. (1998a,b) and ERP studies by Johnson et al. (1998a) and Wilding (1999) are beginning to provide constraints on possible interpretations. Because in both the blood flow and ERP studies significant activation was detected in right frontal cortical areas and scalp for correctly rejected new items, these activities (and the regions from which they are recorded [BA 9, 46]) cannot reflect retrieval success, but rather may be involved in "retrieval verification or monitoring processes or perhaps even in anticipation of subsequent trial events" (Buckner et al., 1998b; p 163). The far-frontal subcomponent of the EM effect, this one negative-going, within the time period of the right frontal activation but of shorter duration (i.e., 600–1,000 ms) has also been observed in CSD mapping studies of recognition (Johnson et al., 1998a). Its focus around the frontal poles means that it may correspond to blood flow activations seen bilaterally in the same general location (BA 10). While no specific retrieval-related processes have been associated with frontal pole activation in the blood flow studies, speculating that it represents some kind of supportive or guidance function in the recovery of episodic information fits well with the fact that blood flow activations have been reported to occur in BA 10 for both verbal and non-verbal retrievals during both old/new recognition and cued recall.

Finally, long duration (500–1,800 ms), left inferior frontal scalp activity has been observed during both episodic cued recall and semantic stem completion (Johnson et al., 1998b). These areas of scalp activity correspond well to hemodynamic activations during semantic retrieval in BAs 44 and 45. Note that activation does not appear in these areas in hemodynamic studies but this may be due to the fact that many of these investigations create their episodic scans by first subtracting the activations obtained in a semantic recall scan. As is clear from the ERP results, such a subtraction would remove the left inferior frontal activity from the episodic scan. Moreover, semantic retrieval during episodic cued recall is not unexpected, as one retrieval strategy might be to first generate viable completions (semantic processing) and then subject the retrieved items to a recognition test (i.e., generate and recognize; Jacoby and Hollingshead, 1990).

This summary of major aspects of the EM effect is not meant to be exhaustive. Undoubtedly, as more complex paradigms, denser electrode arrays, and more detailed surface voltage as well as CSD mapping studies are employed, new aspects of the EM effect will be discovered. Moreover, common brain regions activated in ERP and hemodynamic studies could be more precisely localized, as stated earlier (see Scalp-Recorded Event-Related Potential), by employing a source localization strategy in which the Tailarach and Tournaux (1988) coordinates from blood flow activations in the same or similar paradigms are used to "seed" dipole locations. One can then determine if the resulting modeled scalp distribution is similar to that for any aspect of memory-related activity obtained in ERP studies. Such convergent assessments are obviously in their infancy and much more work needs to be done.

SUGGESTIONS FOR FUTURE RESEARCH

A major difficulty in relating ERPs to hemodynamic phenomena is the strikingly different temporal scales of each and the fact that there is, for several ERP components, no necessary isomorphism between surface activity and the underlying intracranial generators. Nonetheless, this review suggests that there are clear correspondences between the ERP and hemodynamic data with respect to the major variables that have been common to investigations in both domains (e.g., encoding/retrieval; episodic/semantic; Remember/Know; item/source memory). Similarity in the modulation of hemodynamic and ERP activity by common experimental manipulations is one of the stronger, albeit indirect, methods for identifying linkages between these two imaging modalities (see Luck, 1999, for an extended discussion). This method has been employed by a few investigative teams in memory (Rugg et al., 1998c), as well as other areas of psychophysiological research (e.g., Friedman and Fabiani, unpublished observations; Heinze et al., 1994; Menon et al., 1997; Opitz et al., 1999a). However, it is important to note that the brain areas identified by hemodynamic measures and those presumed to be measured by ERP techniques may not be the same, even though interpretations of this type may be plausible. A great deal of further work will be required before the validity of these kinds of inferences are known with certainty.

The ERP mapping studies reviewed here have demonstrated that widespread cortical and subcortical networks combine to support encoding and retrieval of item and source information. However, ERP mapping studies are in their infancy and are still performed with relatively few electrode sites (e.g., 16–32), yielding poor resolution (see Srinivasan et al., 1998). Future studies with dense electrode arrays (64–128 channels) are bound to reveal much finer grained information on different aspects of memory-related ERP activity and the corresponding brain areas that are active during encoding and retrieval. There is also a clear need for more CSD analyses. To date, however, less than a handful of such investigations have been published (e.g., Johnson et al., 1998a,1998b). Nevertheless, even these few studies have shown much greater spatial detail than is available from the voltage maps of the same data. This disparity between surface voltage and CSD maps clearly indicates that subcortical areas are recruited during encoding, and both recognition and recall tasks. Note, however, that subcortical contributions to either encoding or retrieval will always be better revealed by the voltage maps.

There is also a clear need in the ERP studies to look at shorter epochs in the mapping analyses in order to determine more precisely the onsets and durations of the active areas. The approach in which long temporal windows are used to quantify ERP effects appears to have been borrowed from a method in which difference waveforms were used and the entire duration of the difference was treated as a single component. This may, in fact, be the case, but this approach may also obscure the presence of multiple, successive shorter duration components.

As has been argued by others (e.g., Luck, 1999), converging data from different imaging modalities will be required to more fully appreciate the temporo-spatial processing of mnemonic information by the brain. As previously suggested, the hemodynamic and ERP data should be recorded, to the extent possible, in the same subjects using the same experimental design. Moreover, event-related fMRI would be the preferred technique as correspondences between ERP and hemodynamic measures, in terms of effects of the experimental variables, would be easier to determine. With respect to sources of ERP components, several dipole modeling techniques are available (Koles, 1998) and could be used to infer, in combination with hemodynamic areas of activation, common brain regions activated during these memory procedures. As stated above, several investigators have already begun to apply this logic (Heinze et al., 1994; Nenov et al., 1994; Rugg et al., 1998c; Woldorff et al., 1999). This combination has the potential for providing a more informed brain source imaging of cognitive activity in the intact human brain.

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