

# Neural Substrates of Remembering: Event-Related Potential Studies<sup>☆</sup>

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## Introduction

### Memory Subtypes

Remembering does not refer to a unitary ability. Rather, remembering can be fractionated into a set of component processes that are expressed in different combinations under different circumstances. Analyses of memory in healthy individuals and in patients with memory impairments have revealed a set of distinct memory functions that can be assessed using different memory tests. Various theoretical schemes have been used to categorize the memory phenomena measured in these tests, emphasizing either behavioral, cognitive/representational, neural, or subjective criteria. Taxonomies of memory have thus helped to guide research into fundamental questions about memory. Beyond taxonomies, however, we must seek a comprehensive understanding of memory by describing the component processes in both cognitive and neural terms, by clarifying the relationships between cognitive and neural descriptions, and by showing how neurocognitive processes produce memory behavior and associated conscious experiences.

Amnesic patients have specific impairments in declarative memory, the ability to remember facts and events from the past, as assessed in recall and recognition tests. In contrast, other categories of memory phenomena, as listed in [Table 1](#), are not impaired in amnesia. Expressions of declarative memory tend to coincide with the potential for making the metamemory judgment that memory is being expressed—the awareness of remembering. For these reasons, declarative memory is usually regarded as fundamentally distinct from other expressions of memory.

Information can also be held in awareness for an extended period of time, while rehearsed and/or manipulated. Nonetheless, our emphasis here is on memory phenomena that take place when information that was initially encoded is later brought back to mind after a delay, which is what [William James \(1890, pp. 648\)](#) termed secondary memory.

The neural substrates of remembering can be examined in healthy human volunteers using a variety of noninvasive neuroimaging techniques. In particular, recordings of event-related potentials (ERPs) have been used to monitor the activity of the brain during memory tasks. These experiments have made significant headway in identifying neurocognitive processes that are responsible for memory and in specifying processes engaged in association with different memory feats.

Our goal in this chapter is to examine how ERP research has shed light on various processes. We emphasize memory processes that contribute to declarative memory, but we also include the related memory phenomena of priming, given that

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**Table 1** A memory taxonomy based on findings in amnesic patients

Type of memory	Behavioral outcome	Findings in patients with amnesia
<i>Declarative memory</i>	Recall and recognition of episodes and facts (i.e., episodic memory and semantic memory)	Impaired storage, causing deficits in new learning and in remembering information acquired prior to onset of amnesia
<i>Immediate memory</i>	Information available while kept in mind by continuous rehearsal (e.g., verbal working memory)	Preserved if performance is not supported in part by retrieving declarative memories for the rehearsed information
<i>Nondeclarative memory</i> (a large category that includes nonassociative learning, classical conditioning, category learning, habit learning, as well as the following)		Generally preserved, but with some notable exceptions
Perceptual priming	Speeded or more accurate responses in a priming test, based on item-specific or perceptual representations	Preserved if performance is not contaminated by declarative memory
Conceptual priming	Speeded or more accurate responses in a priming test, based on association-specific or conceptual representations	Preserved in some cases, but further investigation is required, particularly across stimulus domains
Skills	Behaviors that improve gradually with practice, including cognitive skills (e.g., reading mirror-reversed text) and motor skills	Preserved when skill acquisition is accomplished without reliance on declarative memory (i.e., not most skills learned outside laboratory circumstances)

dissociations between priming and declarative memory have provided important clues about why declarative memory is distinctive (see section [Using Event-Related Potentials to Contrast Memory Subtypes](#)).

### The Event-Related Potential Technique

Neurons in the human brain generate electric fields that vary moment to moment. When these electric fields are sampled via recording electrodes connected to an amplifier system, the resultant electroencephalographic record—the electroencephalogram (EEG)—shows voltage changes over time and can provide indications of the functioning of networks of neurons as cognitive processing unfolds. EEG recordings from electrodes placed on the scalp are used in a variety of clinical and research contexts.

To examine EEG activity associated with stimulus processing, signal-averaging methods applied to EEG recordings can be used to produce ERPs. Whereas ongoing EEG signals can vary in magnitude on the order of tens of microvolts over a few seconds, ERPs can be extracted so as to observe signals much smaller than 1  $\mu$ V. When a set of EEG responses that are time-locked to a particular class of stimuli are averaged in this way, EEG signals unrelated to stimulus processing tend to decrease because they do not occur at a consistent time relative to the time of stimulus onset. ERPs thus reveal electrical signals produced during the course of stimulus processing, to the extent that such signals are not averaged out due to temporal variability. Signal averaging can be performed with respect to any class of repeated event occurring at a known time. ERPs elicited by stimulus events are viewed as a time series of voltage changes following stimulus onset, which is conventionally referred to as “time 0.” ERP waveforms thus consist of a series of positive and negative deflections, the timing and waveshape of which vary with the nature of the stimuli, and the neural operations performed in response to the stimuli. Some ERPs, such as the brainstem auditory evoked potentials produced during the first 10 ms after a click, have very small amplitudes and require hundreds of stimulus repetitions to obtain a signal-to-noise ratio sufficiently high to permit reliable quantification. Other ERPs, such as some associated with cognitive processing, can be several microvolts in amplitude and occur over a time interval of several hundreds of milliseconds. Typically, averaging over 30–100 stimulus events is required to observe reliable effects of experimental variables in psychological experiments, depending on the amplitude and reliability of the EEG signals in question and on the presence of other EEG signals and EEG artifacts of various sorts (for further methodological details, see [Rugg and Coles, 1995](#); [Luck, 2014](#)).

ERPs can be most readily measured by examining the positive and negative deflections (peaks and troughs) that occur at various poststimulus time points. However, the entire waveform is most likely composed of the summation of neural activity from many distinct sets of neurons in the service of many different functions. Ideally, a complex ERP waveform would be decomposed into a series of ERP components, each of which bearing a unique and systematic relationship to a unitary neurocognitive function. In practice, however, the component structure of an ERP waveform is difficult to discern. Given this strict definition that requires a component to be identified with a unique neurocognitive function, it would be unwise to accept the assumption that each deflection corresponds to a particular component. There may be some cases when a hypothetical component may be adequately measured by examining a deflection. In other cases, deflections are based on the summation of multiple components, which themselves are unknown, such that the amplitude and latency of the composite peak does not provide a valid characterization of any of the individual components. Accordingly, the identification and measurement of specific ERP components can be problematic.

ERP waveforms can nonetheless be quantified in several different ways. Putative components can be identified based on a combination of factors, including latency, polarity, amplitude, distribution, and most importantly, relationships to experimental parameters. ERPs can also be quantified for specific latency intervals without making a priori assumptions about the components that might be present, but with an emphasis instead on differences between experimental conditions. When this approach is followed,

the experimental manipulations play a critical role in focusing the analysis on neurocognitive functions that can be manipulated across conditions. Valid conclusions can be drawn based on such analyses, given that some conclusions are orthogonal to the challenge of determining whether specific aspects of the ERP display a convincing correspondence with ERP components that have been described previously. Although component identification can be informative, it may not be feasible in memory paradigms when a large number of components overlap with each other in the same time range. Indeed, when subjects engage a wide variety of cognitive transactions over an extended time interval, as is likely the case in many of the interesting paradigms cognitive neuroscientists choose to study, it can be misleading to assume that only a very small number of components have been produced. When a large number of ERP components occur simultaneously, specific ERP components cannot always be isolated from one another and separately characterized.

Accordingly, contemporary ERP investigations in cognitive neuroscience no longer exemplify the strict component-centered approach, wherein a chief experimental goal was to understand an ERP component per se. Instead, difference-centered approaches have become prevalent, whereby experimental variables are manipulated based on theory-driven goals concerning specific neurocognitive functions. This shift from a focus on known ERP components to a focus on the thorough understanding of relationships between cognitive operations and neural events has facilitated a greater dialogue between ERP experimenters and scientists working with different methodologies. In the context of memory research, bringing together a variety of methods in cognitive neuroscience has been responsible for significant progress.

### Characterizing Event-Related Potentials

In ERP investigations of human memory functions, a central analysis question in any experiment is often to determine whether two ERPs differ reliably from one another. In other words, the experimenter may ask whether two or more hypothetical psychological processes are associated with reliably different electrical signals. Experimental contrasts are often based on comparing two conditions distinguished by a task manipulation, stimulus factors, response factors, or some combination. A difference between ERPs can then be described and displayed (Fig. 1).

An ERP difference may be statistically significant over a certain time interval. At any given latency, the difference can have a positive or negative polarity. Across a recording epoch, amplitude will vary with a particular wave shape. When an ERP difference between conditions is characterized in this manner, it may appear to correspond to a systematic enhancement of one ERP deflection over a discrete time interval, or it may appear to encompass a different time interval with a unique wave shape.

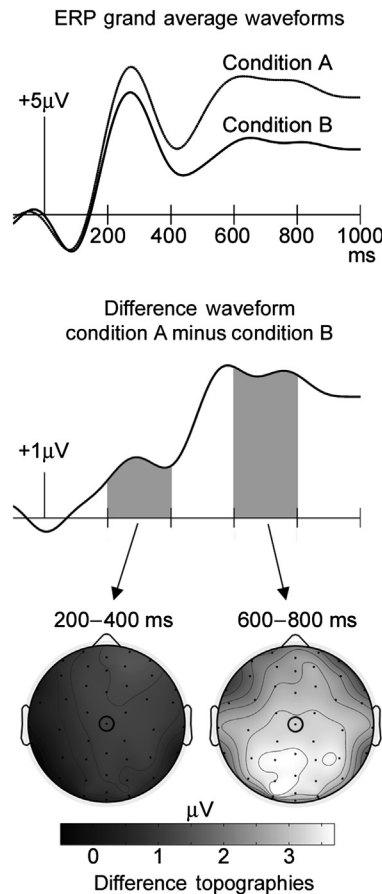
Another important facet of an ERP difference is the distribution of the potential field across multiple electrode locations on the scalp. This topographic information can help investigators make inferences regarding the responsible neural generators. Such inferences involve many assumptions. Models of electric currents and volume conduction of the head can be used to estimate the scalp topography that would be produced by activity at a certain location in the brain. Despite straightforward procedures for solving this so-called forward problem, the inverse problem of determining the brain sources based only on the scalp topography is not soluble, because many different configurations of intracranial generators can produce the same field on the scalp. Various ERP source-modeling procedures can nevertheless be used when considering the anatomical location of the sources of ERPs, although drawbacks of inferring brain sources based on scalp recordings have been heavily debated (McCarthy and Wood, 1985; Kutas and Dale, 1997; Urbach and Kutas, 2002; Wilding, 2006). When theorizing about ERP sources in the brain, it is therefore extremely helpful to bring multiple sources of evidence to bear on understanding the relevant brain structures or systems.

### Advantages and Disadvantages of Using Event-Related Potentials in the Study of Human Memory

ERP methods are noninvasive and relatively inexpensive compared to other neuroimaging methods. As just described, some limited information about relevant neural sources can be extracted from ERP distributions on the scalp. In most circumstances, other methods are preferable for precise neuroanatomical information. ERP waveforms comprise a time-series of voltages between a scalp electrode location and a reference electrode location, so both locations are relevant for determining ERP characteristics. Here, we will emphasize results from recordings using a mastoid or average-mastoid reference, because this recording method is used in a majority of the relevant memory studies. It is important to keep in mind that the mastoid reference is not inactive, as is also the case for any other reference location or any reference digitally constructed. Potentials generated near the reference location influence observed ERP effects in accordance with how currents are conducted through tissue to electrode locations.

ERPs provide useful information even though they do not provide a full view of neural activity. Rather, the EEG is sensitive to activity produced by a restricted set of neurons. These neurons are ones activated synchronously such that extracellular fields produced by their activity can summate. These fields must thus be generated by sets of neurons that are oriented together in such a way to produce electrical fields that will conduct to distant locations where recording electrodes are placed. Much neural activity may be electrically silent at the scalp, in the sense that the EEG may not include signals from some of the active neurons engaged in relevant processing.

A key advantage of ERP methods is that they provide measures of neural activity with very high temporal resolution. The superior temporal resolution of ERPs makes them well suited to examinations of neural events responsible for human memory, which can potentially be monitored on a millisecond-by-millisecond basis. Critical memory processes often unfold within the first second after exposure to a stimulus, and ERPs can allow these processes to be resolved in real time and with randomized trial orders. Delivering trials in a predictable manner or blocking experimental trials, as required in positron emission tomography studies, can



**Figure 1** Visualizing event-related potentials (ERPs). Waveforms averaged across experimental subjects for two experimental conditions, A and B, are considered at a single electrode (top). These waveforms are plotted with time shown on the x-axis going from left to right and with voltage on the y-axis. Here, positive potentials are plotted in the upward direction, although some investigators plot amplitudes in the opposite manner. The time course of the difference in amplitude between these conditions can be visualized as a difference wave (middle), or by averaging over latency intervals of interest (gray shading) for many scalp locations and generating images of the voltage differences across the scalp (bottom). These topographic maps schematically represent the distribution of ERP differences between conditions A and B for the two latency intervals. The head is viewed from above, approximated by a circular shape, with anterior scalp regions toward the top. *Black dots* indicate the locations of recording electrodes. The *black circle* identifies the electrode location used for the waveforms shown. These images can thus demonstrate both temporal and spatial characteristics of an ERP effect.

severely limit the range of memory phenomena amenable to examination. Extended intertrial intervals can also be undesirable to the extent that such procedures do not adequately constrain the timing of relevant cognitive events. In general, when cognitive events can be tightly time-locked to stimulus presentation and temporal blurring across trials decreased, ERP findings have better signal-to-noise ratios and arguably are most useful. Although randomized event-related designs with short intertrial intervals (Burrock et al., 1998) are feasible with functional magnetic resonance imaging (fMRI), ERP signals may be better for isolating brief neurocognitive events or, especially, a series of neurocognitive events that occur closely together in time.

Although ERPs provide temporal resolution that is unsurpassed by that of any other technique in cognitive neuroscience, other neuroimaging modalities that also provide high temporal resolution, including magnetoencephalography (MEG) and monitoring near-infrared optical signals. Such methods hold promise for substantial contributions to the memory literature in the future and may also provide further neuroanatomical insights. Additional information can also be extracted from MEG or from EEG signals by conducting analyses in the frequency domain. For example, stimulus events produce reliable EEG oscillations that may reveal insights into neural activity that are complementary to those available from analyses in the time domain. ERPs can be decomposed into a set of oscillations that occur in phase with stimulus onset and are thus called evoked rhythms. Other oscillations, termed “induced rhythms,” can be time-locked to an event but be out of phase from trial to trial, and therefore are not reflected in time-averaged ERPs. Although there is no widespread agreement on how to distinguish induced from evoked rhythmic activity (e.g., David et al., 2006; Truccolo et al., 2002), a steadily increasing body of literature concerns memory-related cyclic EEG activity (e.g., Klimesch et al., 2001, 2006; Düzel et al., 2003; Hanslmayr et al., 2016). This chapter focuses on evoked signals reflected in ERPs, which provide valid indicators of stimulus-evoked neural activity for at least some categories of processing (e.g., Shah et al., 2004).

## Event-Related Potentials and Memory Encoding

Experiments examining long-term memory generally employ an encoding phase, during which subjects attempt to commit items to memory, followed after some delay by a test phase, during which the success of memory storage and retrieval is evaluated. ERP measures can be collected both at encoding and at test, informing accounts of the relevant neural processing required during these stages. Given that declarative memories change over time, it will ultimately be important to examine relevant processing that can take place at various times between initial encoding and later retrieval. Less work has been devoted to this challenge than to either encoding or retrieval per se, but this area of research is growing rapidly. ERPs at the time of memory reactivation can be predictive of subsequent memory performance (Bridge and Paller, 2012; see section [Interactions Between Memory Formation and Memory Retrieval](#)). Furthermore, memory reactivation during sleep also plays an important role in determining future memory performance, as monitored through ERP recordings during sleep (e.g., Rudoy et al., 2009; Staresina et al., 2015).

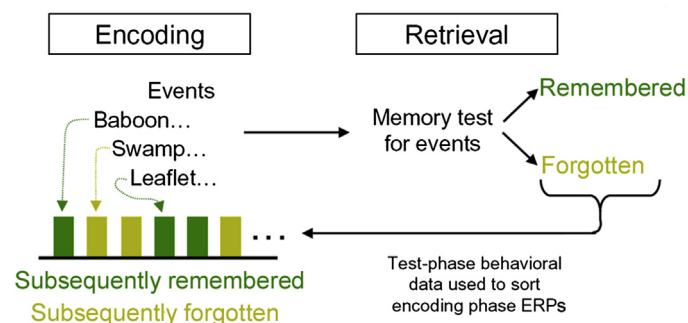
The focus of most ERP studies of memory has been on explicit memory for episodes. Some studies have examined autobiographical memories formed outside the laboratory or memories for general semantic knowledge learning over many years. The most commonly used paradigms concern memory for artificial events in a laboratory setting, such as viewing specific words or images. These studies are advantageous because the circumstances of acquisition can be carefully monitored and controlled. As laboratory studies move closer to accurately simulating real-life memory experiences, the artificial nature of experimental paradigms will hopefully become less problematic in placing limitations on interpretations.

### The Difference Measure Approach

One way to isolate brain events responsible for successful encoding is to acquire ERP responses during encoding and sort trials based on subsequent memory performance (Fig. 2). This general method was first reported with ERPs by Sanquist et al. (1980) and can be traced back to earlier work using skin-conductance methods. Indeed, many sorts of signals can be used in subsequent memory analyses. The term Dm has been used to refer to neurophysiological difference measures found by sorting trials on the basis of subsequent memory performance (Paller et al., 1987). This term provides a convenient way to refer to the various phenomena that can be demonstrated using these methods (e.g., Dm for free recall, Dm for recognition, Dm for pure familiarity), and also avoids prejudging whether the differences reflect variations in a known ERP component. Subsequent memory analyses can be conducted with different encoding requirements, different types of memory tests, and different retention intervals—and all of these parameters may influence the results. Dm potentials observed with different task, stimulus, and subject parameters can presumably index various neurocognitive operations to the extent that these operations influence what information will later be remembered.

Observing reliable Dm effects generally requires that multiple criteria are met, including some interitem variability in encoding strength such that a sufficient number of items are subsequently remembered and a sufficient number of items are subsequently forgotten. Logically, Dm effects will be greater when ERPs index a larger difference between mean responses in these two conditions. Dm analyses can thus gain power when confidence or other graded measures of retrieval success is considered. Ideally, a substantial polarization will be present in successful versus unsuccessful encoding operations. Furthermore, temporal dynamics must also be suitable, such that processing that influences later memory performance is well time-locked to stimuli presented for encoding. It is also important to note that multiple memory-building processes can operate during study, and only those that are relevant to the specific test format used to define the Dm will be identified using this method. Considerations of test format and overlap between operations relevant to study and test are therefore critical when measuring and interpreting Dm effects (Bauch and Otten, 2012).

In many Dm studies, positive potentials maximal over parietal regions were found to be greater for later-remembered items than for later-forgotten items at approximately 400–800 ms. These effects have sometimes been attributed to ERP components such as

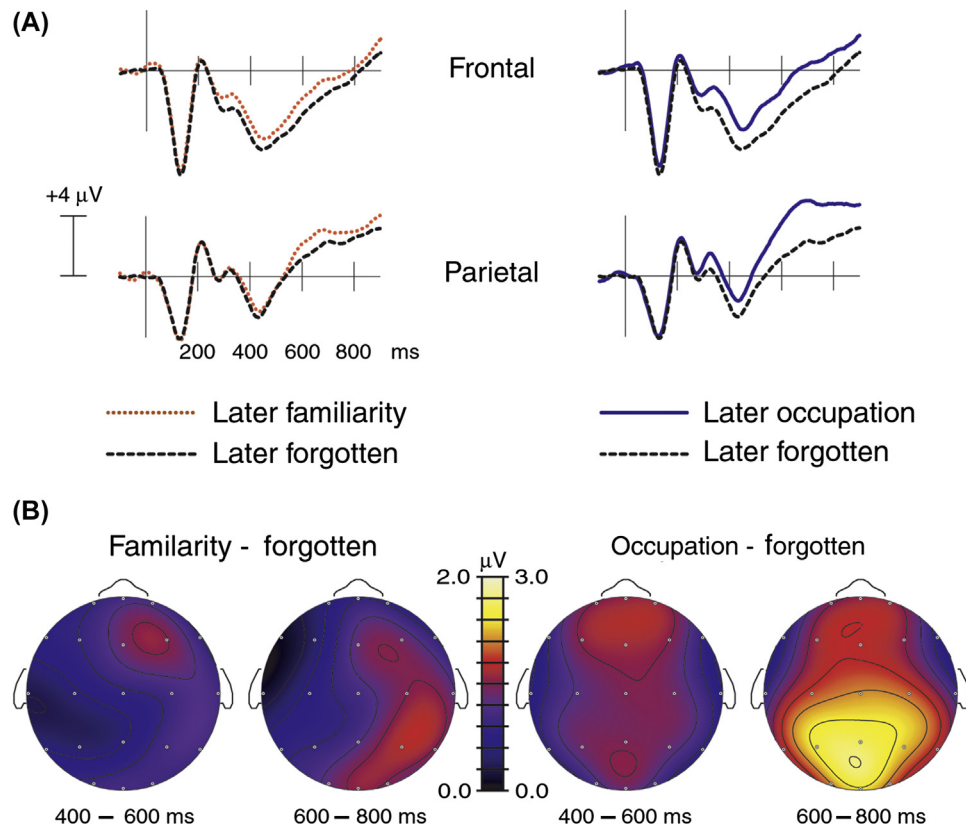


**Figure 2** Schematic of the Dm or subsequent memory methodology. During an encoding phase, neuroimaging measures are recorded while subjects attempt to remember stimuli. During the subsequent retrieval phase, memory tests for these stimuli are administered. Performance on these tests is used to classify study-phase stimuli and corresponding neural measures into two categories, subsequently remembered and subsequently forgotten. A comparison between neural correlates of these two conditions thus yields neurophysiological differences computed on the basis of subsequent memory performance, *Dm*. ERP, event-related potential. Figure adapted from Paller, K.A., Wagner, A.D., 2002. Observing the transformation of experience into memory. *Trends Cogn. Sci.* 6, 93–102.

P300 or the late-positive complex (e.g., [Karis et al., 1984](#); [Fabiani et al., 1986](#)). In the past three decades, Dm has been observed in many paradigms, including tests of recall and recognition (reviewed in [Wagner et al., 1999](#); [Paller and Wagner, 2002](#)). A favored cognitive hypothesis about these Dm findings is that they reflect superior elaborative encoding for items later remembered. Semantic elaboration is well known to be effective for producing strong episodic memories, and deeper semantic elaboration often corresponds with larger late posterior potentials. The nature of Dm effects due to elaboration can differ depending on the nature of the elaborative processes, however, in that frontal slow waves rather than late parietal-maximum positive potentials have been observed when subjects attempt to remember lists of unrelated words by generating novel associations to create relationships among items ([Fabiani et al., 1990](#); [Friedman, 1990](#)). Creating novel associations likely requires a larger contribution from working memory processes supported by frontal cortex compared to elaborating on the inherent meaning of a single word.

In an investigation of memory for faces, results revealed distinct Dm effects depending on the type of memory retrieval engaged during the subsequent memory test ([Yovel and Paller, 2004](#)). As shown in [Fig. 3](#), a robust Dm that was bilaterally symmetric at posterior scalp locations was found to predict later recollection (when subjects recognized the face and recalled information previously associated with the face), whereas a smaller right-sided Dm predicted later familiarity (when subjects recognized the face but could retrieve no additional information). In another study of face recognition, Dm differed for the same-race faces compared to different-race faces, shedding light on how differences in individuation at the time of memory encoding can give rise to the common occurrence of better remembering for people from one's own race ([Lucas et al., 2011](#)).

Based on another type of Dm demonstrated in a few studies with words, it appears that left-frontal potentials starting at approximately 500 ms can be sensitive to the amount of information bound into a memory trace at encoding (reviewed in [Friedman and Johnson, 2000](#)). The magnitude of these potentials may be proportional to the amount of information remembered subsequently. One hypothesis is that these sustained positive potentials reflect the operation of strategic encoding processes.



**Figure 3** Representative Dm effects for two categories of memory. Two different memory experiences can be assessed after people learn to associate novel faces with randomly assigned occupations. [Yovel and Paller \(2004\)](#) categorized trials according to whether faces were forgotten or remembered with reference to the face alone with no contextual retrieval (familiarity) or remembered with retrieval of both the face and the paired occupation (recollection). ERPs (event-related potentials) were recorded when subjects studied these face/occupation pairs and relatively more positive ERPs were found to predict later memory. These Dm effects are displayed at two representative electrodes in (A) and the scalp topography of these effects appears in (B). Scalp maps are of the head viewed from above, with anterior oriented toward the top. Comparing the two effects, Dm for recollection exhibited a bilateral topography with larger amplitudes spanning a longer time interval, whereas Dm for familiarity was smaller, briefer, and restricted to right posterior locations. Figure adapted from Yovel, G., Paller, K.A., 2004. The neural basis of the butcher-on-the-bus phenomenon: when a face seems familiar but is not remembered. *NeuroImage* 21, 789–800.

In addition to stimulus-evoked neural processing that leads to later remembering, tonic brain activity that precedes the onset of a stimulus has also been linked to the efficacy of memory encoding. For example, in a study reported by Otten et al. (2006), ERPs over the front of the head were more negative for subsequently remembered versus subsequently forgotten items in the interval preceding stimulus onset by several hundred milliseconds. These electrophysiological findings have an important implication for investigations of encoding using other methods such as fMRI; anticipatory as well as stimulus-locked neural activity could be blurred together due to the poor temporal resolution of fMRI. Procedures are thus needed to separate fMRI correlates of these dissociable cognitive events. Although anticipatory Dm activity has not been extensively investigated, one compelling hypothesis is that it reflects working memory control operations, given that such operations can lead to better encoding of a declarative memory.

Gonsalves and Paller (2000b) showed that ERPs at encoding can reflect mistaken memories as well as accurate ones. ERPs were found to reflect the vivid visual imagery when subjects viewed a single word and visualized the referent of the word, and this activity was found to be relevant to false remembering. Trials were categorized according to whether or not subjects subsequently claimed (erroneously) to have seen a picture of the visualized object, revealing that these posterior ERPs were predictive of whether or not a false memory for that item would happen in the test phase. ERPs thus revealed encoding activity that was partially responsible for the later mistake. In contrast, large and more widespread ERPs were predictive of accurate memory for viewed pictures.

On the whole, Dm effects may index a group of encoding operations that lead to superior memory, including detailed perceptual analysis, rote rehearsal, semantic elaboration, mental imagery, and so on. Further research is needed to clarify how Dm varies as a function of stimulus materials and type of memory test, and to precisely specify the relationship between these electrical measures and specific encoding operations. A fruitful approach for future neuroimaging studies, for example, would be to directly manipulate hypothetical mnemonic processes to determine the relative contribution of different operations to Dm effects. The usefulness of this approach for advancing explanations of memory formation can be exemplified by an fMRI investigation (Reber et al., 2002). Subjects were instructed to intentionally remember some words and intentionally forget others. By virtue of this directed-forgetting manipulation, fMRI correlates of the differential intention to remember were identified in addition to standard Dm effects based on retrieval success. fMRI Dm effects commonly include increased activity in both inferior prefrontal cortex and the medial temporal lobe (MTL). Although encoding condition and the probability of successful subsequent memory retrieval were correlated in this study, prefrontal activity was preferentially associated with encoding effort, whereas MTL activity was preferentially associated with success (Reber et al., 2002). Results thus identified the specific contribution to encoding of mnemonic operations guided by the intent to remember a word and supported by left inferior prefrontal cortex.

### Intracranial Dm Effects

Electrodes implanted into the brains of patients who are candidates for surgery to remove an epileptic focus provide a special opportunity to combine the real-time temporal resolution of the ERP technique with superior spatial localization. This approach has limitations, however, in that activity can only be sampled from a limited number of brain regions, as electrodes are placed only where required for clinical purposes. In addition, generalizability can be questioned because recordings are made from a small number of individuals who have typically taken antiseizure medication for many years to try to control abnormal electrical activity in the brain. Results can nonetheless be used to inform theoretical accounts of the neural basis of memory formation.

In an ERP study reported by Fernandez et al. (2002), recordings were made from two areas within the MTL, the hippocampus, and an adjacent cortical region near the rhinal sulcus. Based on research with amnesic patients and with nonhuman animals, the hippocampus together with adjacent parahippocampal, entorhinal, and perirhinal cortical regions has been considered as essential circuitry for the formation of declarative memories, in conjunction with widespread neocortical regions that are ultimately responsible for memory storage (Squire et al., 2004). Potentials recorded from the rhinal region (entorhinal and/or perirhinal cortex) and hippocampus predicted subsequent free recall of visual words. The rhinal Dm peaked approximately 400–500 ms after word onset and was thought to be associated with the extent to which words were processed semantically. The hippocampal Dm, in contrast, started later and was taken to reflect the successful binding of multiple features into memory following semantic analysis.

These results support the notion that distinct MTL regions perform unique mnemonic operations. Other intracranial ERP studies have demonstrated a range of phenomena that may also reflect important memory functions (Heit et al., 1988; Grunwald et al., 1998; Allison et al., 1999; Guillem et al., 1999; Paller and McCarthy, 2002; Trautner et al., 2004; Engel et al., 2005; Viskontas et al., 2006). For example, a complex pattern of rhinal–hippocampal synchronization and desynchronization was found via frequency-domain analyses of the same intracranial data (Fell et al., 2001). EEG synchronization and desynchronization in various other brain locations has also been observed to correlate with subsequent memory performance (Sederberg et al., 2003, 2006; Hanslmayr et al., 2016). Furthermore, single-unit firing patterns in the hippocampus have been shown to vary as a function of subsequent memory performance (Cameron et al., 2001).

As is the case for scalp-recorded effects, intracranial Dm effects can also be identified in the interval preceding stimulus onset during study. Increases in hippocampal theta power prior to stimulus onset have been a focus of these studies (Fell et al., 2011), although lower frequency effects in a variety of cortical regions have also been identified (Haque et al., 2015).

### Event-Related Potentials and Memory Retrieval

Whereas veridical memory performance is only possible if some information was initially encoded, the nature of memory is also a function of events taking place at the time of retrieval. Furthermore, the most interesting distinctions between types of memory

(e.g., declarative memory and priming) and memory processes (e.g., recollection and familiarity) are largely realized at retrieval. This is the time when one can engage in the conscious experience of remembering that can approximate reliving a past event.

### Identifying Correlates of Recognition

In most ERP studies of memory retrieval, electrophysiological responses are recorded while recognition is tested. In a recognition test for episodes studied during an encoding phase, subjects must discriminate old (repeated) items from novel items. ERP correlates of episodic memory (sometimes termed episodic memory effects or old/new effects) are commonly identified by contrasting ERP responses elicited by old items to those elicited by new items. Much effort in ERP studies of memory has been devoted to attempting to elucidate the specific memory processes that give rise to old/new effects.

Measures of neural activity obtained when people remember episodes are often interpreted in light of theories that posit two distinct recognition processes: recollection and familiarity. Recollection involves the recognition that an event has occurred in the past along with the retrieval of specifics regarding the prior occurrence, thereby guiding the conscious experience of remembering. In contrast, familiarity denotes recognition of prior occurrence that remains unsubstantiated by retrieval of any specific detail. Familiarity can lead to a feeling of knowing in the absence of the ability to bring to mind any additional information. Recollection and familiarity are connected with the concepts of source memory and item memory, in that source memory concerns the spatiotemporal context and various other features that can support recollection, whereas familiarity for a stimulus might be driven by retrieval limited to item memory.

An experimental procedure known as the remember/know paradigm has been employed extensively in attempts to identify neural correlates of recollection and familiarity. Subjects are cued to introspectively classify their recognition of old stimuli as “remember” if specific study-phase detail is simultaneously brought to mind or as “know” if no such detail is retrieved. The remember/know response categories have been taken as generic indices of recollection and familiarity, respectively. Under some experimental conditions, however, remember/know responses may correspond to varying degrees of memory strength instead of qualitatively different memory processes (Eldridge et al., 2002). In addition, it is possible that results obtained from this procedure are highly influenced by nonmnemonic variables, such as the capacity to introspect accurately. Great care is thus needed in applying this method. Confidence in results can be increased with convergent support from multiple methods, such as with memory judgments based on source information.

Indeed, a useful approach to separating ERP components related to recollection and familiarity is to test memory for specific source information based on the experimental context at encoding. For example, subjects may encode words spoken by either a male or female voice, and later be tested with visual words and asked to recall the gender of the original voice. In general, correct source retrieval can be used to indicate recollection. Incorrect source retrieval with correct recognition, however, is not always a good indicator of familiarity, given that recollection may be supported by retrieval of information other than the specific source information in question.

Distinct ERP effects have been linked to three types of mnemonic processes associated with memory retrieval. These findings are outlined in the following three sections.

### Recollection and Source Memory

The most consistently reported finding in recognition studies is that ERP amplitudes to old items are greater than those to new items from approximately 400–800 ms over much of the scalp. These effects typically show a maximal difference over midline or left parietal scalp locations. The amplitude of these differences generally increases with increasing memory strength based on various behavioral indices (e.g., recognition confidence). Compared to recognized items (hits), both old items that are forgotten (misses) and new items that are correctly identified (correct rejections) tend to elicit smaller ERPs.

Early investigations of these old/new ERP effects endorsed a variety of hypotheses concerning their functional significance, including associations with memory strength (Johnson et al., 1985), relative familiarity (Rugg, 1990), contextual retrieval (Smith and Halgren, 1989), and processes that do not contribute to recognition judgments (Rugg and Nagy, 1989). Despite this lack of consensus about the meaning of these ERPs during these years, a common assumption was that the effects included modulation of two ERP components: N400 potentials and P300 potentials (e.g., Halgren and Smith, 1987).

An early study that convincingly associated ERPs with recollection utilized a level-of-processing manipulation at study (Paller and Kutas, 1992). Behavioral results showed that this manipulation influenced recall and recognition performance, in that semantic encoding requiring visual imagery produced superior memory compared to encoding focused on letter information. In contrast, the same level of priming (Table 1) was observed on an implicit memory test of word identification for both encoding tasks. ERPs recorded during the implicit memory test were compared between the two conditions defined by the task assigned at encoding, and corresponding differences were interpreted as ERP correlates of recollection. This ERP difference based on encoding task began at a latency of 500 ms and was only present for words that were successfully identified in the test phase. Unlike typical old/new ERP effects, this effect could not be attributed to differences associated with priming because priming was matched between the two encoding conditions. Furthermore, behavioral evidence obtained at debriefing showed that subjects noticed that words from the encoding phase appeared during the word-identification test, even though this was irrelevant to their task. In other words, subjects were cognizant of specific contextual information with respect to some of the words in the word-identification test that repeated from earlier in the experiment. The combination of behavioral and

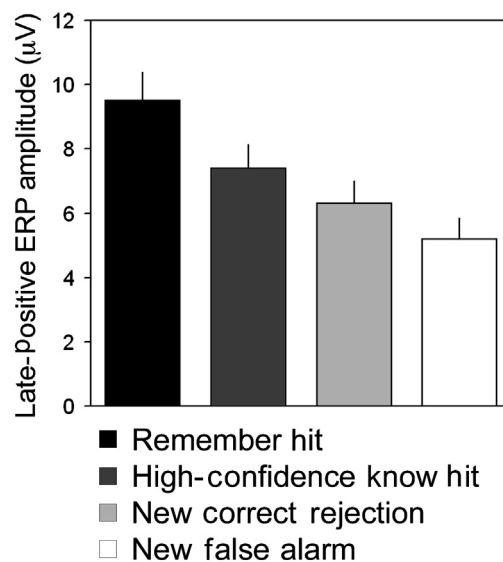
electrophysiological evidence thus provides strong support for the authors' two key inferences that (1) incidental recollection took place during the test phase, particularly when word meaning had been encoded deeply and that (2) ERPs were sensitive to this differential processing associated with recollection.

Further studies using the same strategy in experimental design have substantiated the association between ERPs and recollection and extended the results to the use of other encoding tasks and memory tests (Paller et al., 1995), words presented in the auditory modality (Gonsalves and Paller, 2000a), and other types of stimuli such as faces (Paller et al., 1999). These late parietal ERPs can thus be taken as signals of the successful retrieval of episodic memories linked with conscious remembering (reviewed in Friedman and Johnson, 2000; Paller, 2000).

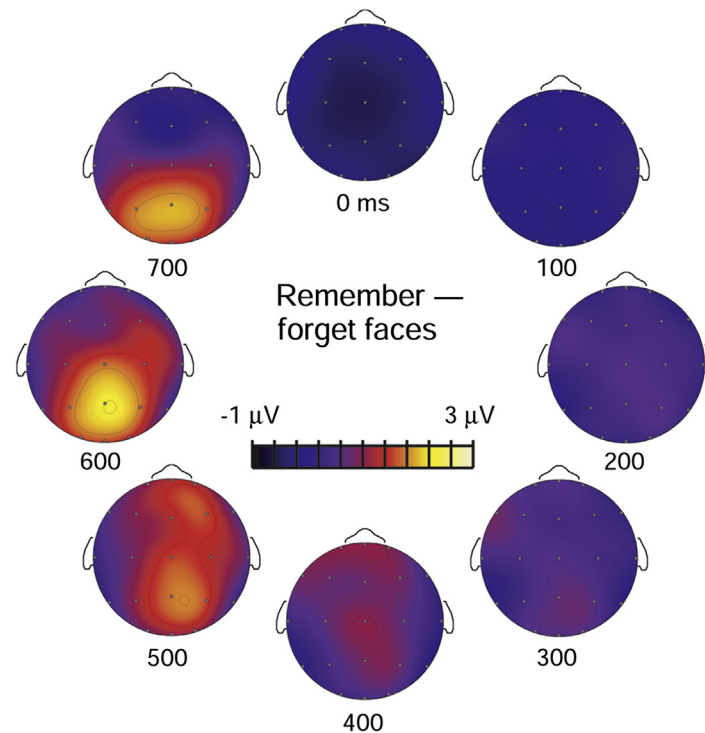
Results from remember/know as well as source-memory paradigms have also been used to associate late parietal ERPs with recollection. Late parietal ERP amplitudes are often found to be greater for remember compared to know responses and know responses compared to new trials. Importantly, there have not been convincing demonstrations that the distribution of late parietal ERPs differ between remember and know responses, indicating that these ERPs may index a neurocognitive operation that differs only quantitatively between recollection and familiarity conditions (e.g., Smith, 1993). Similarly, correct source judgments elicit greater late parietal amplitudes compared to incorrect source judgments, and incorrect source judgments greater than new trials, without qualitative differences in scalp distribution (e.g., Wilding and Rugg, 1996; Trott et al., 1999). Indeed, using nonverbal stimuli that effectively limit confounding influences of semantic processing on the memory-related ERP, Voss and Paller (2009b) found that late parietal ERP amplitudes vary with memory strength across confidence and accuracy levels (Fig. 4).

In addition to corroborating the connection between recollection and late posterior potentials, many experiments have targeted ERP correlates of source and item memory to understand contextual memory in its own right. Experimental contexts have included speaker gender (Senkfor and Van Petten, 1998); performed, watched, or imagined actions (Senkfor et al., 2002); background figures (Guo et al., 2006); spatial location (Van Petten et al., 2000); and stimulus color (Cycowicz et al., 2001), among others.

Results from memory-disordered patients have also confirmed associations between successful recollection and late-positive ERPs. Amnesic patients exhibited impaired recollection as well as reduced or absent late-positive amplitudes (e.g., Olichney et al., 2000, 2006; Addante et al., 2012). In addition, administration of benzodiazepine drugs to healthy subjects prior to encoding creates a temporary state of amnesia, and following this manipulation, both recollection and late parietal potentials are severely disrupted (e.g., Curran et al., 2006b). Taken together, evidence taken from a variety of experimental paradigms thus converges on the conclusion that recollection is a distinct expression of memory that reliably occurs with a particular ERP signature (Fig. 5).



**Figure 4** Late-positive potentials scale with the success/strength of explicit memory. During a recognition memory test, amplitude of the late-positive component (LPC) was greatest when subjects reported recollection of an old item (remember hit) and was reduced when subjects reported high-confidence familiarity (high-confidence know hit). Correct rejection of a new item requires some memory retrieval of old items to support the memory discrimination and late-positive amplitude for this condition (new correct rejection) was lower than for high-confidence familiarity of old items. Late-positive amplitude was least when subjects falsely endorsed new items as old (new false alarm), indicating no successful memory retrieval. This pattern of late-positive event-related potential (ERP) amplitudes across conditions indicates that these potentials signal the success/strength of explicit memory retrieval. Stimuli were novel geometric shapes, which limited contamination of these ERPs by conceptual/linguistic processing. Data are from Voss, J.L., Paller, K.A., 2009b. Remembering and knowing: electrophysiological distinctions at encoding but not retrieval. *NeuroImage* 46, 280–289.



**Figure 5** Late-positive potentials index conscious recollection. Posterior, positive potentials from 300 to 800 ms after the presentation of faces that were previously encoded with the instruction to remember (remember faces) were greater than for faces that were encoded with the instruction to forget (forget faces). Each remember face was also presented with a short biographical vignette, and subjects were highly accurate at recollecting this information when cued by the corresponding face. Behavioral results also showed that recognition was better for remember faces than for forget faces whereas priming did not differ. Thus, these late-positive potentials index recollective processing uncontaminated by priming. Data are from Paller, K.A., Bozic, V.S., Ranganath, C., Grabowecy, M., Yamada, S., 1999. Brain waves following remembered faces index conscious recollection. *Cogn. Brain Res.* 7, 519–531.

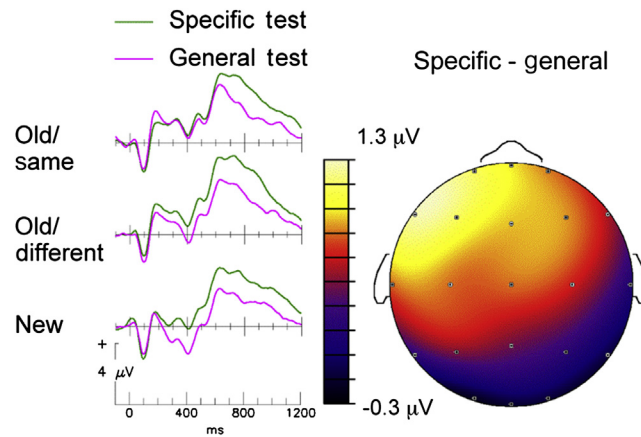
### Postretrieval Processing

Another memory phenomenon may be indexed by positive potentials at prefrontal scalp locations beginning approximately 500 ms after stimulus onset and extending for up to several seconds. These potentials often display a right-sided distribution. They do not index retrieval success, in that they tend to be similar for both successful and unsuccessful retrieval attempts. Instead, these frontal potentials are thought to index effortful retrieval processing, manipulation of working-memory contents, and/or post-decisional mnemonic processing such as further evaluation (Fig. 6).

The functional significance of these late frontal potentials was difficult to decipher, partly due to the absence of a direct connection with retrieval success. Experimental manipulations of retrieval demands, however, were useful for clarifying the cognitive operations indexed by these potentials. In one study, drawings of common objects were encoded, and these objects were presented again at test in either the identical format or perceptually altered (Ranganath and Paller, 1999). Subjects performed one of two tests that differed in the demands placed on effortful retrieval of perceptual detail. In the highly demanding test, subjects responded “old” only to objects in the identical format whereas in the less demanding test objects were to be endorsed as old regardless of any format alterations. Late frontal potentials were larger in the highly demanding test than in the less-demanding test for both categories of old as well as for new stimuli (Fig. 6). These potentials thus appeared to track retrieval effort as manipulated across these two recognition tests. Subsequent investigations have confirmed this interpretation (Ranganath et al., 2000; Ranganath and Paller, 2000; Leynes, 2002; Herron et al., 2016), supporting the view that late frontal potentials track strategic processing that accompanies retrieval, a process likely mediated by prefrontal cortex. Hemispheric loci of late frontal potentials can also vary as a function of retrieval demands, with a right-to-left shift accompanying an increase in the complexity of the retrieved information (Johnson et al., 1997; Nolde et al., 1998).

### Recognition With Pure Familiarity

Attempts to associate the memory experience of familiarity with specific ERPs have been most controversial. Results from many studies have been taken to indicate that familiarity is generically indexed by a negative potentials peaking approximately 400 ms poststimulus, an N400-like potential with reduced amplitudes (i.e., more positive ERPs) for old compared to new items,



**Figure 6** Late frontal potentials associated with retrieval processing. ERPs (event-related potentials) to drawings of common objects were compared between a highly demanding (specific) recognition test and a less demanding (general) recognition test. Waveforms (left) showed a relative positivity for the specific test compared to the general test for all three stimulus classes in the experiment: objects that are perceptually identical to one in the study phase (old/same), objects that are perceptually altered from one in the study phase (old/different), and entirely novel object pictures. The corresponding ERP topography was computed over all conditions for the latency interval from 500 to 1200 ms. These late frontal potentials were maximal over the left anterior scalp, but in other experiments have also been found to be bilaterally symmetric or maximal over right anterior scalp. Figure adapted from Ranganath, C., Paller, K.A., 1999. Frontal brain potentials during recognition are modulated by requirements to retrieve perceptual detail. *Neuron* 22, 605–613.

especially at anterior locations. Beginning with the work of Düzel et al. (1997), many researchers have proposed that the frontal N400 old/new effect indexes recognition with familiarity, in contradistinction to recollection (reviewed in Curran et al., 2006a). Whereas late posterior potentials are greater in circumstances in which recollection is greater (for example, following semantically deep vs semantically shallow encoding tasks), the frontal N400 old/new effect is generally found to be insensitive to such manipulations (e.g., Rugg et al., 1998a,b). In addition, frontal N400 potentials have been associated with phenomenological familiarity as indexed by the remember/know paradigm (e.g., Düzel et al., 1997; Woodruff et al., 2006) and have been found not to scale with the amount of recollection during tests of source memory (e.g., Wilding, 2000). In sum, frontal N400 potentials are sensitive to recognition success but not to manipulations that effect recollection and thus are widely described in the extant ERP literature as a general correlate of familiarity.

On the other hand, there is reason to doubt this generalization about frontal N400 potentials, because the majority of findings used to argue in favor of this association are indirect (see below and Paller et al., 2007; for a review). Specifically, the logic of interpretation has generally been that frontal N400 potentials reflect recognition memory and do not behave as a neural correlate of recollection, and so the inference made has been that they therefore index familiarity. A direct challenge to this fragile interpretation arose with the identification of intact N400 repetition effects in amnesic patients (Olichney et al., 2000). A reasonable generalization is that amnesia disrupts familiarity, in the sense that a patient with severe amnesia does not behave as if people and various objects they encounter feel familiar. This generalization also stands on sound empirical footing (Knowlton and Squire, 1995; Yonelinas et al., 1998). Thus, one might expect patients with amnesia to exhibit reduced N400 old/new effects if these effects indeed index familiarity. Olichney et al. (2000) thus suggested that frontal N400 potentials might instead reflect the operation of conceptual implicit memory processes that can be engaged incidentally during recognition testing. In general, special steps are necessary to isolate the contribution of separate but potentially co-occurring memory phenomena to neural correlates of recognition memory, as discussed in detail in the next section.

Several studies have examined the phenomenon of familiarity without recollection using faces, as in the classic example described by Mandler (1980) as the butcher-on-the-bus phenomenon. The butcher's face may seem extremely familiar yet not be identified when seen in an unusual context, such as on the bus—whereas in the butcher's shop familiarity is more likely to occur together with memory for additional episodic and semantic information that uniquely identifies the specific person. Yovel and Paller (2004) used a variation of the remember/know paradigm to segregate trials for separate analyses of recollection and familiarity. Recognition with familiarity, compared to correct rejections of new faces, co-occurred with late-positive ERPs that were maximal at midline parietal locations; recognition with recollection co-occurred with late-positive ERPs that were much larger in amplitude, spanned a longer time interval, and showed a slightly more anterior topography. MacKenzie and Donaldson (2007) conducted a similar study and found statistically significant topographic differences; familiarity was associated with late posterior ERPs and recollection with larger and more anterior ERPs. However, a third study (Curran and Hancock, 2007) used a more heterogeneous mixture of faces (i.e., faces with different racial and ethnic features) and failed to replicate this pattern; instead attributing an N400 effect to familiarity for faces. Of course, it is plausible that characteristics of the people shown could influence the extent to which repeated faces engage conceptual priming, although this idea deserves further study. In sum, most studies of familiarity experiences during face processing associated familiarity with late posterior ERPs, not with the earlier frontal N400 potentials described in prior

studies that used words or nameable objects. Further studies are needed to determine whether this divergence can be explained by showing that familiarity entails different neural events for verbal versus facial stimuli, that heterogeneity of face stimuli plays a crucial role, or whether alternative interpretations of frontal N400 potentials are viable (see section [Identification of Neural Correlates of Conceptual Priming](#)).

Results from a limited number of studies can be taken as tentative evidence that familiarity may be indexed by potentials occurring earlier than frontal N400s ([Tsivilis et al., 2001](#); [Curran and Dien, 2003](#); [Duarte et al., 2004](#); [Friedman, 2004](#); [Diana et al., 2005](#); [Voss and Paller, 2009a](#)). These potentials occur between 100 and 300 ms but otherwise closely resemble FN400 potentials—frontal ERPs to old items are more positive than to new items. Like FN400 potentials, these earlier frontal potentials have been associated with familiarity based on indirect evidence: the effect is present in association with phenomenological reports of familiarity and does not scale with recollection. More evidence is needed to determine if these potentials indeed index familiarity as opposed to other potentially co-occurring memory phenomena, such as various forms of priming and the initiation of memory search (e.g., [Diana et al., 2005](#)).

### Interactions Between Memory Formation and Memory Retrieval

Although memory formation and memory retrieval have generally been studied in isolation, a growing literature seeks to understand their relationships. For instance, many of the ERP Dm effects identified at study resemble similar retrieval effects identified at test, and so it is possible that these ERPs reflect memory processing common to memory formation and retrieval. [Chen et al. \(2014\)](#) studied covariation of ERP study-phase Dm effects with test-phase retrieval effects and identified a complex pattern of interrelationship, whereby late-positive Dm ERPs correlated with frontal N400 retrieval correlates, and frontal slow wave Dm ERPs correlated with the late-positive ERP effect at test. These findings of relationships between temporally and topographically distinct ERP correlates at study and test suggest that ERP correlates of memory formation predict those of memory retrieval. However, there was no one-to-one mapping of memory formation ERP correlates with superficially similar memory retrieval ERP correlates, suggesting complex relationships.

Another way to probe memory formation and retrieval relationships is by considering their immediate interactions. For instance, memory retrieval and memory formation can occur together during memory testing when new memories are formed of the retrieval event. [Bridge and Paller \(2012\)](#) identified ERP correlates of the interaction of memory retrieval and memory formation using a three-stage paradigm. In the first stage, objects were studied at unique locations. In the second stage, subjects recalled the locations by attempting to replace the objects in their original locations. Because recall we are not perfect, this provided the opportunity to develop a new memory for the (incorrectly) recalled location. During the third stage, a final memory test was given to measure whether object location memory more closely matched the originally studied object locations versus the incorrectly recalled locations from stage 2. During the second stage, typical late parietal ERP effects were identified for successful recollection, and later-onset frontoparietal ERPs predicted whether performance on the final memory test reflected a new memory formed for the incorrectly recalled locations. This pattern of results indicates that ERP correlates distinct from successful retrieval signal the interaction of encoding and retrieval that produces new memories for retrieved information.

Intracranial ERPs have also identified interactions of memory formation and retrieval. For instance, [Reber et al. \(2016\)](#) had subjects memorize word pairs that shared indirect links (e.g., the pair “tree-dog” and “tree-foot” include the indirect link of “dog-foot” via shared association with “tree”). When the second word pair (“tree-foot”) is presented during study, retrieval of the first indirectly related pair (“tree-dog”) occurred, such that subjects later endorsed the indirect link (“dog-foot”) during memory testing. ERPs recorded from the hippocampus during presentation of the second word pairs demonstrated rapid-onset positive enhancements when the indirect links were later endorsed, thus providing direct ERP correlates of the interaction of retrieval with memory formation.

### Using Event-Related Potentials to Contrast Memory Subtypes

Memory performance undoubtedly reflects the operation of a variety of neural systems. Multiple memory systems or processes make variable contributions to performance on different mnemonic tasks. ERP investigations are especially well-suited for identifying the occurrence of these variable contributions and thereby disentangling the operation of distinct memory components. Indeed, we must first come to understand these separate components before we can work out how their interactions ultimately produce memory abilities.

Here, we will highlight one distinction that has been particularly amenable to investigation with ERPs, that between explicit memory and forms of implicit memory known collectively as priming. In an explicit memory test, specific reference is made to remembering information learned earlier. In an implicit test of memory, in contrast, no reference is made to learning episodes, but rather, memory is demonstrated via a change in performance in a certain task due to a prior event that may or may not be consciously remembered. Contrasts between these two broad categories of memory phenomena have been very prominent in memory research over the past two decades. Performance on explicit memory tests is typically disrupted in cases of amnesia, as described earlier. On the other hand, many types of implicit memory have been shown to be preserved in amnesia. Priming is a form of implicit memory that is indexed behaviorally as faster or more accurate responses on specialized priming tests, independent of conscious memory for study episodes. The most common types of priming tests are used to measure perceptual priming

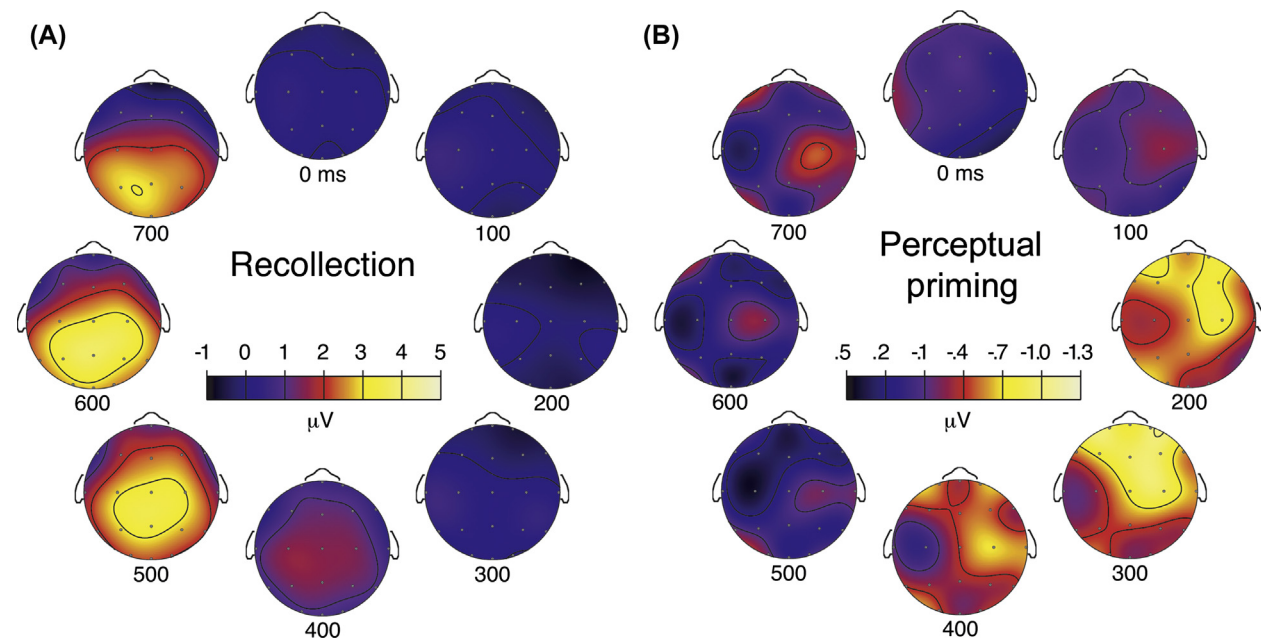
(also called item-specific implicit memory). These behavioral effects are thought to reflect facilitated or more fluent perceptual processing of the physical features of repeated items, distinct from accessing a memory for the full episode in which the item occurred. A different set of mechanisms may be responsible for some types of priming (i.e., conceptual priming, novel-information priming, new-association priming, association-specific priming, or cross-domain priming), and in some of these cases priming may not be preserved in amnesia, although this is a topic under continuing investigation.

When memory tests are given to healthy individuals, performance may be guided by explicit memory, implicit memory, or by some combination. In this sense, memory tests may not be “process-pure.” In addition to acknowledging that behavioral measures in memory tests can reflect multiple memory processes, it is important to note that neural measures such as ERPs are liable to be influenced by multiple memory processes as well. Moreover, neural measures can reflect memory processes whether or not those processes influence behavioral performance. In either implicit or explicit memory tests, ERPs can reflect neurocognitive processes responsible for both types of memory. Experimental manipulations that selectively influence the operation of distinct components of memory are thus essential. Otherwise, ERP or other neuroimaging results cannot be unequivocally associated with one type of memory versus the other.

### Direct Comparisons Between Recollection and Perceptual Priming

Isolating neural correlates of perceptual priming uncontaminated by those of conscious remembering is problematic because of the difficulty of preventing subjects from recalling prior episodes during priming tests. Similarly, the automatic processing that supports perceptual priming may occur during recognition tests, even if behavioral measures of priming are not obtained, and this processing can potentially be reflected in neural measures accompanying recognition.

To isolate ERP correlates of perceptual priming, Paller et al. (2003) used a condition in which faces were encoded only to a minimal extent such that priming occurred in the absence of recognition. Subjects viewed each face for 100 ms at a central location while simultaneously a yellow cross was shown unpredictably in one of the four quadrants 1.8 degrees from fixation. While maintaining central fixation, subjects attempted to discriminate between two subtly different types of yellow crosses, and further stimulus processing was disrupted via backward masking. On a subsequent test, recognition of these minimally processed faces was not significantly better than chance. Perceptual priming for these faces, however, was observed behaviorally on two implicit memory tests. The logic of this design was thus that ERPs elicited by these faces could conceivably reflect neural events responsible for perceptual priming, whereas contributions from recognition processes would be negligible. Faces in another condition were presented for a longer duration, without disruptive perifoveal visual discriminations or backward masking, and were recognized at above-chance levels. These two conditions thus provided a direct comparison during subsequent memory testing between ERPs associated with conscious memory for faces and ERPs associated with perceptual priming. Recognition-related neural correlates included late-positive potentials (Fig. 7A), closely resembling responses previously associated with face-cued



**Figure 7** ERP (event-related potential) correlates of recollection and perceptual priming. The ERP difference between recollected faces and new faces is displayed in (A). The difference between primed but not remembered faces and new faces is displayed in (B). Differences are averaged over 100 ms intervals starting at the latency indicated underneath each topographic map. Light colors indicate positive difference potentials in (A) and negative difference potentials in (B). Figure adapted from Paller, K.A., Hutson, C.A., Miller, B.B., Boehm, S.G., 2003. Neural manifestations of memory with and without awareness. *Neuron* 38, 507–516.

recollection (Paller et al., 1999; Paller, 2000), whereas perceptual priming was associated with a relative ERP negativity over anterior recording electrodes from approximately 200–400 ms after face onset (Fig. 7B). Spatiotemporally distinct ERPs of opposite polarities were thus associated with conscious remembering versus perceptual priming. This pattern of neuroimaging findings complements neuroanatomical dissociations identified in amnesic patients; the results imply that implicit access to memory is supported by processing within a network of brain regions that is qualitatively distinct from that supporting conscious access to memory.

Evidence for the independence of implicit and explicit memory can also be derived from contrasts between neural correlates of encoding responsible for later perceptual priming versus recollection. Schott et al. (2002) used deep/semantic versus shallow/non-semantic encoding conditions, followed by an ingenious, two-stage procedure to assess memory. Three-letter word stems were presented in an explicit memory test (i.e., cued recall), but subjects were encouraged to guess if they could not remember a studied word so that priming might also occur. After each stem was completed, subjects indicated using strict criteria whether they recognized the word from the encoding phase. Trials were categorized as showing priming if the subject produced the word at the completion stage but failed to endorse it as an old word (i.e., priming-without-recognition). Trials were categorized as remembered when the correct response was made at both stages, and as forgotten if not produced at the completion stage. Subsequent memory analyses thus revealed a Dm for priming that took the form of a relative ERP negativity over central and frontocentral locations approximately 200–400 ms after word onset (resembling ERP correlates of perceptual priming identified during memory testing, e.g., Paller et al., 2003). Furthermore, Dm for priming was distinct from ERP differences between deep versus shallow encoding as well as from Dm for recognition, which both included relatively positive potentials at later intervals with different topographies. Collectively, these results (along with those from a follow-up study using fMRI, Schott et al., 2006) constitute critical steps in characterizing the neurocognitive relationship between expressions of explicit memory and expressions of perceptual implicit memory.

### Identification of Neural Correlates of Conceptual Priming

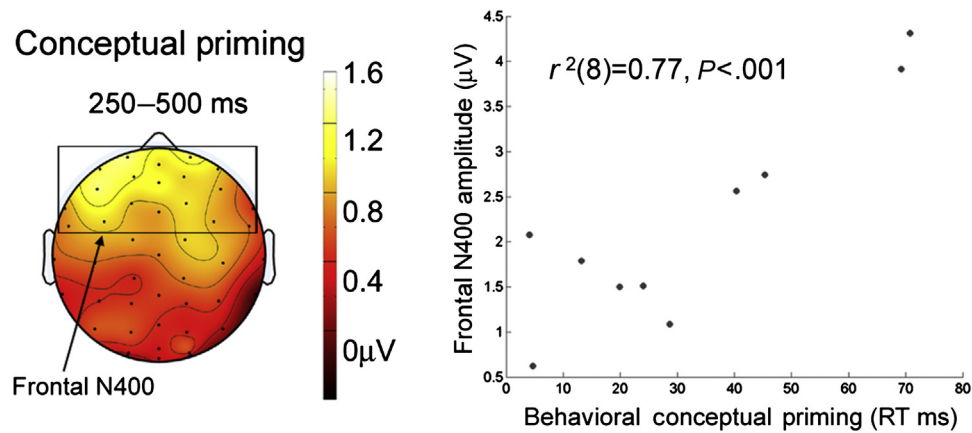
Another form of priming known as conceptual priming can occur whenever meaningful stimuli are repeated. Behavioral measures of conceptual priming are similar to those of perceptual priming in that they can occur in the absence of awareness of remembering and typically take the form of faster or more accurate responses to a specific stimulus. These alterations of behavioral responses are thought to reflect facilitated processing of stimulus meaning, and potentially support some of the short-term mnemonic operations that are preserved in amnesia, such as language comprehension.

Because the neural processing that supports conceptual priming can occur whenever meaningful stimuli are repeated, regardless of whether a behavioral test of conceptual priming is provided, it is possible that neural activity associated with conceptual priming occurs incidentally during tests of recognition memory for meaningful stimuli. As reviewed earlier, frontal N400 potentials at retrieval have been postulated to index the explicit memory capability termed familiarity. The finding that similar potentials are intact in amnesic patients (Olichney et al., 2000), however, raised the possibility that frontal N400s instead reflect a form of memory that is not disrupted in amnesia. Olichney et al. (2000) proposed that residual conceptual priming in amnesic patients could be reflected by frontal N400 potentials. It is thus possible that frontal N400 potentials do not index familiarity but instead reflect conceptual priming that occurs concurrently with explicit memory (Paller et al., 2007).

One study directly examined this issue by using celebrity faces to elicit neural correlates of conceptual priming and explicit memory (Voss and Paller, 2006). Conceptual priming was manipulated by presenting associated biographical information along with a subset of celebrity faces. Later, electrophysiological recordings were obtained while subjects rapidly discriminated celebrity faces from other faces. Evidence for conceptual priming consisted of faster and more accurate responses to the subset of faces previously presented with biographical information. A controlled ERP comparison was provided by a counterbalanced set of celebrity faces that were previously presented without corresponding biographical information. Electrophysiological responses were obtained during the discrimination test and were characterized according to both conceptual priming as well as ratings of explicit memory for celebrities obtained in the last phase of the experiment. Conceptual priming was strongly associated with frontal N400 potentials (Fig. 8) whereas explicit memory was related to late-positive potentials at posterior locations.

Another set of studies capitalized on the fact that only conceptually meaningful stimuli can support conceptual priming, whereas both meaningful and meaningless stimuli can support explicit familiarity. These studies use abstract visual shapes and obscure words, which vary in meaningfulness from person to person. Across studies, only those items judged by subjects as relatively meaningful supported behavioral measures of conceptual priming and frontal N400 repetition effects (Voss et al., 2010a,b; Voss and Paller, 2007; Gao et al., 2015). In contrast, familiarity was robust for all items, including those judged as relatively meaningless. For these items, late-positive ERP effects were also robust, indicating that familiarity can be indexed by these potentials, irrespective of stimulus meaningfulness. These studies are advantageous because they involved behavioral measures of both familiarity and conceptual priming, which were essential for validating their distinct neural correlates. Other studies have used only familiarity measures, but nonetheless provide converging evidence that frontal N400 ERPs are not identified when relatively meaningless stimuli are repeated in memory tests (e.g., Danker et al., 2008; Voss and Paller, 2009a,b).

These results attest to the likelihood that neural activity related to conceptual implicit memory is commonly produced in memory experiments designed to monitor explicit memory (see Voss et al., 2012). Therefore, this contamination of neural signals is also possible in studies using other methods to measure brain activity, such as fMRI (Voss and Paller, 2008). Furthermore, the prominent hypothesis that frontal N400 potentials are unique neural signatures of familiarity must be called into question, because it might partially (or entirely) reflect the operation of implicit memory (Voss and Federmeier, 2011). Much work will be needed to



**Figure 8** Neural correlates of conceptual priming include frontal N400 potentials. The ERP (event-related potential) contrast between famous faces based on whether corresponding conceptual information was primed in an earlier phase of the experiment is shown topographically for the latency interval from 250 to 500 ms (left). The frontal N400 effect is indicated. The magnitude of these potentials (quantified in each subject at the electrode exhibiting the greatest frontal N400 conceptual priming effect) was correlated across subjects with the magnitude of conceptual priming indexed behaviorally (right). Data are from Voss, J.L., Paller, K.A., 2006. Fluent conceptual processing and explicit memory for faces are electrophysiologically distinct. *J. Neurosci.* 26, 926–933.

accurately elucidate the neural substrates of these memory processes, but doing so is critical for understanding the neural substrates of familiarity and of priming. This approach further highlights the necessity of employing experimental manipulations and multiple behavioral measures that can allow for valid associations between neuroimaging measures and memory functions, such that this information can be used to build an accurate characterization of the brain processes that support human memory performance.

### Future Contributions of Event-Related Potential Studies to Memory Research

Remarkable progress has been made in identifying component processes of human memory capabilities and characterizing corresponding neural substrates of memory. However, there is much more to be learned so as to demystify the cognitive, biological, and phenomenological facets of memory. Given that a memory cue can unleash such a rapid flood of relevant neural events that precipitate remembering, ERP techniques have an important role to play in this endeavor.

One theoretical keystone involves identifying factors that make implicit and explicit expressions of memory unique. ERPs have been extremely useful in this regard and thus have a continuing role to play in conjunction with other methods of cognitive neuroscience. In addition to elucidating differences between conscious and nonconscious memory expressions, a deeper understanding of this issue will allow us to characterize how these distinct forms of memory interact in a variety of situations to drive memory performance. Whereas our understanding of such interactions has hitherto derived primarily from behavioral evidence obtained from healthy individuals and memory-impaired patients, physiological data are also needed. Valid descriptions of the neural bases and neural dynamics of explicit and implicit forms of memory are essential for understanding their functional relationships.

The detailed theoretical account of memory that can be achieved in this manner will ultimately be important for maximizing our memory capabilities in everyday life. Among the possible practical applications of memory research, possibilities for memory rehabilitation are critical in neurological and psychiatric diseases that affect memory and during the course of healthy aging. Indeed, there is a large literature on ERP correlates of age-related cognitive changes (Bharani et al., 2016; James et al., 2016; Wang et al., 2012) and on memory disruptions and preservations in neurodegenerative disease (Ally et al., 2009) that has progressed to the point of biomarker testing for conditions such as Alzheimer's disease (Cecchi et al., 2015; Quiroz et al., 2011). Much of human experience revolves around bringing to mind events from the past. Explorations of remembering via electrical recordings of brain activity may thus lead to a better understanding of ourselves.

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