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When encoding yields remembering: insights from event-related neuroimaging

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To understand human memory, it is important to determine why some experiences are remembered whereas others are forgotten. Until recently, insights into the neural bases of human memory encoding, the processes by which information is transformed into an enduring memory trace, have primarily been derived from neuropsychological studies of humans with select brain lesions. The advent of functional neuroimaging methods, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), has provided a new opportunity to gain additional understanding of how the brain supports memory formation. Importantly, the recent development of event-related fMRI methods now allows for examination of trial-by-trial differences in neural activity during encoding and of the consequences of these differences for later remembering. In this review, we consider the contributions of PET and fMRI studies to the understanding of memory encoding, placing a particular emphasis on recent event-related fMRI studies of the Dm effect: that is, differences in neural activity during encoding that are related to differences in subsequent memory. We then turn our attention to the rich literature on the Dm effect that has emerged from studies using event-related potentials (ERPs). It is hoped that the integration of findings from ERP studies, which offer higher temporal resolution, with those from event-related fMRI studies, which offer higher spatial resolution, will shed new light on when and why encoding yields subsequent remembering.

Keywords: subsequent memory effect; episodic encoding; episodic memory; event-related potentials; fMRI; PET

1. INTRODUCTION

In the course of a typical day, humans experience many complex events: perceiving faces and other objects, reading words and text passages, interpreting the meaning of spoken phrases, and the like. Yet, at the end of the day, only a subset of these experiences are memorable, with many of the day's events having been forgotten. To understand human memory, it is critically important to determine why some experiences can be later remembered, whereas others are subsequently forgotten. Considerable behavioural and neuropsychological evidence indicates that the ability to remember a given experience is affected by many factors, including the kinds of processing operations that are engaged at the time of encoding and retrieval, and interactions between encoding and retrieval operations (for a review and discussion, see Schacter 1996; Tulving 1983). In the present review, we focus on the neural correlates of encoding that predict later memorability.

Encoding refers to the processes that transform incoming information into an enduring memory representation. Until recently, understanding of the neural correlates of encoding processes has primarily come from studies of patients with focal lesions to particular brain regions. Such studies have yielded important insights into the nature of various aspects of memory, and have been indispensable for dissociating different forms of memory (e.g. explicit versus implicit, declarative versus non-declarative) and relating them to specific brain regions (for reviews, see Gabrieli 1998; Schacter *et al.* 1993; Squire 1992). However, studies of brain-damaged patients have not provided unambiguous evidence regarding the neural correlates and functional characteristics of encoding processes because of conceptual difficulties that arise when attempting to determine whether patients' impairments are attributable to an encoding deficit, a retrieval deficit, or both (for a discussion, see Schacter & Tulving 1982).

The advent of functional neuroimaging techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) has provided a new opportunity to gain insight into the neural correlates of encoding processes. PET and fMRI are similar techniques in the sense that both rely on changes in haemodynamic responses that are correlated with changes in neuronal activity: fMRI is sensitive to oxygenation-level-dependent changes in the magnetic properties of blood, and PET is sensitive to local changes in blood flow. Relative to other neuroimaging methods, such as electrophysiological recordings of event-related potentials (ERPs) that are time locked to the onset of particular stimuli, PET and fMRI offer higher spatial resolution but lower temporal resolution (although recent

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advances suggest that fMRI also may offer high temporal resolution; see Menon *et al.* 1998). Importantly, in contrast to neuropsychological studies of brain-injured patients, these functional neuroimaging techniques allow a separation between encoding and retrieval processes. By scanning experimental participants during the encoding phase of a memory experiment, it is possible to examine which brain regions show increased or decreased activity during particular types of encoding tasks, and to correlate levels of activity during the encoding phase with levels of subsequent memory performance.

Until recently, fMRI and PET studies of encoding have relied on 'blocked' experimental designs. In blocked-design studies, target stimuli from different encoding conditions (e.g. deep versus shallow encoding, intentional encoding versus passive viewing, encoding of novel versus familiar stimuli) are presented in separate 'blocks', and brain activity is averaged across the encoding task performed during a particular block. Although such designs allow conclusions about the neural correlates of encoding tasks that tend to produce, on average, higher or lower levels of subsequent memory performance, they do not allow examination of the trial-by-trial encoding operations that influence later remembering. Recent developments in analysing fMRI data, however, now make it possible to examine such trial-by-trial differences (Buckner *et al.* 1996; Dale & Buckner 1997; Josephs *et al.* 1997; Konishi *et al.* 1996; Zarahn *et al.* 1997; reviewed by Rosen *et al.* 1998). In event-related fMRI studies, all experimental trial types can be rapidly intermixed in a random or pseudo-random format in a manner similar to that typically used in behavioural and ERP studies of cognition. Critically, in addition to allowing the intermixing of experimental conditions, event-related fMRI methods also permit analysis of data based on the participant's response—analysis that is directly related to trial-by-trial differences in thought or behaviour.

Application of event-related fMRI procedures to the study of memory encoding has allowed, for the first time, the analysis of fMRI trials sorted by subsequent memory, such that encoding trials can now be separately considered based on whether or not a participant is able to later remember the encoded item. Such an analysis permits identification and functional characterization of the neural regions that predict subsequent memory, that is, regions that demonstrate a differential response during the encoding of events that are subsequently remembered compared with that during the encoding of events that are subsequently forgotten. As discussed below, prior to the advent of fMRI, there existed a rich ERP literature exploring electrophysiological differences based on later memory (the 'Dm' effect, Paller *et al.* 1987*a*). Although there currently are few event-related fMRI studies of the Dm effect, results from the initial studies complement this ERP literature by identifying, with high spatial resolution, specific frontal and temporal regions that predict subsequent memory.

The purpose of this review is to consider the contributions of event-related neuroimaging methods to our understanding of the neural correlates of memory encoding. We begin by briefly surveying blocked-design fMRI and PET studies of encoding, and then turn our attention to event-related fMRI studies of the Dm effect. After discussing these initial fMRI studies, we then extensively review the ERP Dm literature. We believe that consideration of the earlier insights obtained using ERP methods may serve to inform and constrain future event-related fMRI studies. We suggest further that a more complete understanding of memory encoding will be derived through the integration, both within and across studies, of results from methods offering high spatial resolution (fMRI) and methods offering high temporal resolution (ERP or magnetoencephalography (MEG)).

2. BLOCKED-DESIGN fMRI AND PET STUDIES OF ENCODING PROCESSES

Neuroimaging studies concerned with episodic memory encoding have shown activations in a variety of brain regions under conditions in which participants intentionally or incidentally encode various kinds of target items—words, word pairs, pictures, patterns and so forth (for reviews, see Buckner & Koutstaal 1998; Nyberg 1998; Nyberg *et al.* 1996). Empirical and theoretical attention has tended to focus on the nature of activation in prefrontal and medial temporal cortices during various kinds of encoding conditions. We first briefly summarize evidence from blocked-design PET and fMRI studies concerning prefrontal contributions to encoding and then turn to data concerning the medial temporal region.

Findings from several early PET and fMRI studies of episodic encoding focused attention on the contribution of regions within the prefrontal cortex. The vast majority of these early studies examined prefrontal activation during the encoding of verbal stimuli that have pre-experimental semantic content, such as words and nameable objects. For example, several studies compared brain activity during semantic or 'deep' encoding tasks (e.g. judging whether a word represents an abstract or concrete concept) with brain activity during non-semantic or 'shallow' encoding tasks (e.g. judging whether a word is presented in upper- or lower-case letters). Semantic encoding typically yields, on average, higher levels of subsequent memory performance compared with non-semantic encoding (Craik & Lockhart 1972), raising the possibility that observed activation differences reflect encoding processes that directly influence later remembering. Such studies have consistently revealed greater activation in regions of left inferior prefrontal cortex (Brodmann areas (BA) 44, 45, 47) during semantic compared with non-semantic encoding (e.g. Demb *et al.* 1995; Fletcher *et al.* 1995; Kapur *et al.* 1994; Shallice *et al.* 1994; Wagner *et al.* 1998*b*). Similar patterns of activation have been observed when comparing intentional word encoding with lower-level baseline conditions (e.g. Kapur *et al.* 1996; Kelley *et al.* 1998). These left inferior prefrontal regions are extremely similar to the left prefrontal regions that show activation during tasks that require retrieval from semantic memory, such as generating semantic associates of words (e.g. Fiez *et al.* 1996; Klein *et al.* 1995; McCarthy *et al.* 1993; Petersen *et al.* 1988). These findings strongly suggest that retrieval from semantic memory and verbal encoding into episodic memory share underlying component processes (for more extensive discussion of this point, see Buckner 1996; Nyberg *et al.* 1996). In addition, a subset of these left inferior prefrontal regions,

namely the posterior and dorsal extent of the left inferior frontal cortex (near Broca's area BA 44), are extremely similar to the left prefrontal regions that show activation during phonological working memory tasks (e.g. Awh *et al.* 1996; Paulesu *et al.* 1993), suggesting that the processing of phonological and lexical attributes of stimuli also contributes to event encoding.

As mentioned, in the foregoing and many other studies linking left prefrontal activity with episodic encoding, the target stimuli were verbal materials (for detailed reviews, see Buckner 1996; Nyberg *et al.* 1996; Tulving *et al.* 1994). More recent studies have revealed evidence of homologous right inferior prefrontal activation during encoding of non-verbal information, including faces (Kelley *et al.* 1998; cf. Haxby *et al.* 1996) and abstract visual patterns (Wagner *et al.* 1998*a*). These right inferior prefrontal regions have also been observed in studies of visuospatial attention and visuospatial working memory (for reviews, see Awh & Jonides 1998; D'Esposito *et al.* 1998). Taken together, the results from verbal and non-verbal encoding studies suggest that episodic encoding is facilitated by frontally mediated working memory processes, with the nature of the to-be-learned material influencing which specific working memory operations are recruited (e.g. Buckner 1996; Wagner 1999).

Neuroimaging research has also been concerned with the role of the medial temporal lobe (MTL), including the hippocampus, in episodic encoding processes (for reviews, see Lepage *et al.* 1998; Schacter & Wagner 1999). Despite some early failures to obtain significant MTL activation, a growing number of PET and fMRI studies have reported evidence linking MTL activation with episodic encoding. In a number of such studies, MTL activation has been observed under conditions in which exposure to novel stimulus materials is compared with exposure to familiar materials (cf. Dolan & Fletcher 1997; Gabrieli *et al.* 1997; Rombouts *et al.* 1997; Stern *et al.* 1996; Tulving *et al.* 1996). For example, Stern *et al.* (1996) reported that the posterior aspects of the hippocampus and the parahippocampal gyrus were more active during the intentional learning of visual scenes which had not been previously presented prior to encoding (novel stimuli) compared with the learning of scenes which had previously been presented prior to encoding (familiar stimuli). Similarly, Gabrieli *et al.* (1997) reported evidence that, compared with the incidental encoding of familiar pictures, incidental encoding of novel pictures yielded greater posterior MTL activation situated bilaterally in the parahippocampal cortex. Although these findings suggest a link between MTL activity and novelty detection, several recent studies indicate that MTL activations during encoding extend beyond responses to novelty (e.g. Fernandez *et al.* 1998; Kelley *et al.* 1998; Wagner *et al.* 1998*b*). For example, Wagner *et al.* (1998*b*) reported greater left parahippocampal (and fusiform) activation during a deep encoding task (abstract or concrete judgements about words) compared with a shallow encoding task (upper- or lowercase judgements about words). Finally, as with observations that activation within prefrontal regions is affected by the nature of the material being encoded, there have been reports that the encoding of verbal and non-verbal stimuli are differentially associated with left and right MTL regions (e.g. Kelley *et al.* 1998; Martin *et al.* 1997).

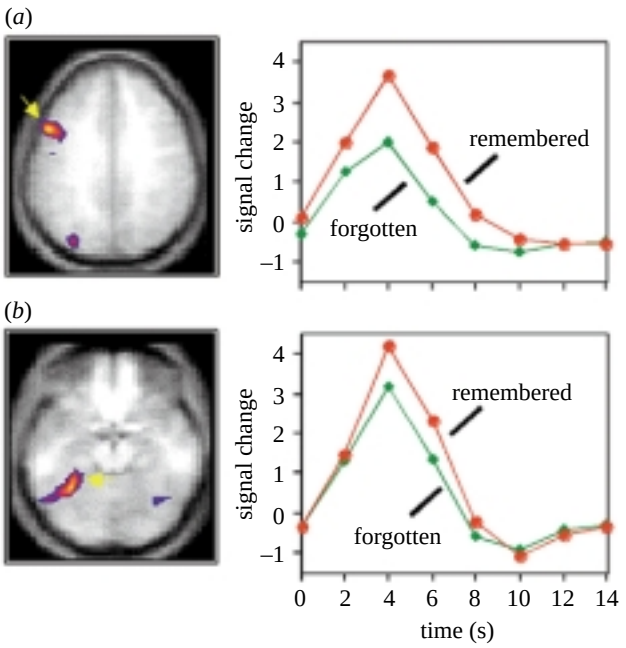

Figure 1. Statistical activation maps and corresponding time-courses from the event-related fMRI study of Wagner *et al.* (1998*b*). Displayed are left frontal and temporal regions that demonstrated a greater response during the encoding of words later remembered (high confidence hit trials) relative to words later forgotten (miss trials). Regions demonstrating this Dm effect included the posterior and dorsal extent of the left inferior frontal cortex (BA 44,6; highlighted by arrow in (*a*)) and the posterior extent of the parahippocampal cortex (highlighted by arrow in (*b*)). In addition to these regions, a Dm effect was observed in left fusiform gyrus (also displayed in (*b*)) and in other left inferior frontal cortices (see text for details).

For example, Kelly *et al.* (1998) observed that posterior left MTL regions were engaged during the encoding of words, and bilateral posterior MTL regions were engaged during the encoding of objects and faces.

Whereas the preceding studies have provided initial insights into the contributions of MTL regions to memory encoding, more recent blocked-design fMRI and PET studies have attempted to examine the correlation between the level of MTL activation across an encoding block and the level of subsequent memory for the items in that encoding block. For example, Fernandez *et al.* (1998) reported an experiment in which participants studied lists of common words. They used a blocked design in which 15 words (three five-word blocks) were studied during scanning, followed by a brief period of distraction and then a free recall test in which participants tried to remember the words from the preceding list. There were 20 repetitions of this study–distraction–test cycle, each time with a new set of target words. Fernandez *et al.* acquired data from seven slices that were perpendicular to the long axis of the hippocampus, extending from the anterior to the posterior extent of the MTL region. They analysed their data by correlating the magnitude of fMRI signals during the five-word encoding blocks with the number of words from each block that were subsequently produced on the free recall test. For 11 out of 13 participants, they found significant positive correlations

between the number of recalled words and signal intensity in posterior hippocampal–MTL regions.

In a separate study, Fernandez *et al.* (1999) used a slightly modified version of the above design to further examine the correlation between MTL activation and later cued recall. In this study, each fMRI scan consisted of six sets of five words each, with the five-word sets separated by approximately 13 s of fixation. Following each 30-word scan, word-stem cued recall was performed, with participants attempting to complete three-letter word-stems (e.g. ENT_) with one of the just studied words (e.g. ENTRANCE). As in the preceding study, Fernandez *et al.* (1999) correlated the level of activation during the encoding of each five-word set with the level of subsequent cued recall for the words from each set. Results revealed that five out of the six participants demonstrated significant activation–subsequent memory correlations in bilateral MTL regions that encompassed the posterior extent of the entorhinal cortex, and three out of the six demonstrated additional correlations in the anterior extent of the entorhinal cortex. Interestingly, the temporal characteristics of the entorhinal response consisted of an initial signal increase prior to onset of each five-word block, perhaps reflecting an anticipatory response, with this level of activation then being sustained across the entire five-word block. This pattern suggests that entorhinal cortex may demonstrate an encoding or attentional state shift that precedes the period of memory encoding (i.e. this modulation is not event related). This shift may affect the recruitment or efficacy of entorhinal encoding operations, thereby affecting subsequent cued recall.

Using a different correlational procedure, Alkire *et al.* (1998) examined the association between regional glucose metabolic rate during the incidental encoding of a block of words and later free recall for the words. They scanned subjects, using PET, while they listened to a repeated sequence of unrelated words. Twenty-four hours later (outside the scanner), subjects attempted to recall the previously studied words. Alkire *et al.* reported a strong positive correlation (+0.91) between activity in a left posterior MTL region, situated in the parahippocampal gyrus, during the encoding phase of the experiment and the number of words recalled on the subsequent memory test. Further, they observed significant correlations in multiple left frontal regions including Broca's area (BA 44, 45) and the ventral extent of the inferior frontal gyrus (BA 47).

3. EVENT-RELATED fMRI STUDIES OF ENCODING PROCESSES

As the § 2 review illustrates, a number of insights into the neural correlates of episodic encoding have been derived from blocked-design PET and fMRI studies. However, the nature of the insights that can be obtained from blocked-design experimental methods are limited because such designs only permit examination of neural activity that is averaged across an entire block of experimental trials. Thus, although it is possible to determine how neural activity differs when performing an encoding task that yields, on average, better relative to worse subsequent memory, it is not possible to determine how trial-by-trial differences in engagement of encoding operations influence later remembering. That is, blocked-design methods do not permit the direct association between event-related differences in neural activity and event-related differences in later mnemonic behaviour (i.e. later remembering), and so cannot directly provide evidence that addresses the question: why are some events later remembered whereas others are later forgotten? The ability to address this question, and many others, requires the analysis of data at the event level. As previously discussed, event-related fMRI methods allow for such a trial-by-trial analysis. These methods have just begun to be applied to the study of memory encoding.

Direct evidence that the magnitude of frontal and MTL activation during the encoding of individual events is associated with subsequent memory for those events comes from two recent event-related fMRI studies (Brewer *et al.* 1998; Wagner *et al.* 1998*b*). Using event-related fMRI methods that allow for the rapid intermixing of experimental trials (Dale & Buckner 1997), we recently conducted a whole-brain fMRI study to determine whether the level of left MTL and prefrontal activation during the encoding of individual words predicts subsequent memory for those words (Wagner *et al.* 1998*b*). In contrast to blocked-design studies that typically vary the nature of the encoding tasks in order to manipulate subsequent levels of memory, this study instructed participants to perform the same encoding task for all learning trials. The experiment consisted of six functional scans, with each scan comprising 80 word trials and 40 visual fixation trials (i.e. participants looked at a crosshair) that were randomly intermixed and presented at a rate of 2 s per trial. For word trials, participants decided whether each word was abstract or concrete. Approximately 20 min after the final scan was completed, participants were given a (non-scanned) recognition test on which they made 'old or new' judgements about studied and non-studied words; when they judged that a word was 'old', they also indicated whether their judgement was accompanied by high confidence or low confidence.

The event-related procedures allowed us to analyse the fMRI data by sorting encoding trials according to whether a word was subsequently remembered or forgotten. The logic of this analysis is identical to that initially reported in ERP studies of the Dm effect (e.g. Sanquist *et al.* 1980; Neville *et al.* 1986), where the encoding trials are assigned to the critical experimental conditions based on the participant's subsequent memory for each word. When high-confidence hits (i.e. 'old' responses to studied words accompanied by high confidence) were compared with misses (i.e. 'new' responses to studied words), we found significant activation in left prefrontal and left temporal regions (figure 1). Within frontal cortex, this Dm effect was observed in an anterior and ventral extent of the left inferior frontal gyrus (approximately BA 45,47), in a more posterior and dorsal extent of left inferior frontal gyrus (approximately BA 44,6), and in the left frontal operculum (approximately BA 47). Within temporal cortex, the Dm effect was observed in the left parahippocampal (approximately BA 36,37,35) and fusiform (approximately BA 37) gyri. To examine whether these effects could be attributed to time-on-task differences (e.g. participants might have

attended longer to words that were subsequently remembered than to words that were subsequently forgotten), a subset of the trials was selected such that response latencies during encoding were matched for subsequently remembered and forgotten items. This analysis revealed the same pattern of greater parahippocampal and prefrontal response for high-confidence hits than for misses as was seen in the overall analysis. In addition, a further analysis (not described in the short report of Wagner *et al.* 1998*b*) that compared high-confidence hits with low-confidence hits again revealed significant left parahippocampal (−25, −37, −6), fusiform (−43, −58, −6), and prefrontal (−43, 13, 21) activations. Thus, the results from this study indicate that one factor influencing the subsequent memorability of verbal experiences is the extent to which the processes mediated by left inferior frontal and left parahippocampal regions are engaged during those experiences.

Complementary results were obtained in an event-related fMRI study of non-verbal encoding conducted by Brewer *et al.* (1998). Participants in this study were shown 24 pictures of indoor and outdoor scenes (the same as those used by Gabrieli *et al.* 1997) during each of four scans, and judged whether each picture depicted an indoor or outdoor scene. Data were acquired using slices orientated perpendicularly to the long axis of the hippocampus, encompassing the posterior extent of the frontal and MTL regions. Thirty minutes later, subjects were given a (non-scanned) recognition test on which they made 'old or new' judgements about previously studied pictures and new pictures. For pictures judged as 'old', participants also indicated whether they possessed a specific recollection of having seen the picture earlier (a 'remember' judgement) or whether the picture just seemed familiar to them (a 'know' judgement, see Gardiner & Java 1993; Tulving 1985). Brewer *et al.* (1998) found that the activity level in bilateral parahippocampal cortex and in the posterior extent of the right inferior frontal gyrus predicted subsequent remembering and forgetting. There was greater activity during encoding for pictures that were 'remembered' with specific details than for pictures that just seemed familiar, and also for familiar pictures compared with forgotten pictures. Thus, one factor influencing the subsequent memorability of non-verbal (pictorial) experiences is the extent to which the processes mediated by right inferior frontal and bilateral parahippocampal regions are engaged during those experiences.

The findings from these event-related fMRI studies, together with earlier findings from blocked-design PET and fMRI studies, suggest that frontal and medial temporal regions may act interdependently to promote the encoding of events into memory (e.g. Wagner *et al.* 1998*b*). The specific frontal and medial temporal regions engaged during encoding appear to depend on the nature of the processes recruited during encoding, with verbal and non-verbal information resulting in recruitment of distinct mnemonic processes. Verbal experiences may be more memorable when semantic and phonological attributes of the experience are extensively processed via participation of left prefrontal regions (e.g. Kapur *et al.* 1996; Wagner *et al.* 1998*b*). Left prefrontal regions may serve to organize these attributes in working memory (e.g. Buckner 1996; Wagner 1999), with this information serving as input to left medial temporal regions. (Note that considerable behavioural evidence indicates that the ability to remember an experience is influenced by the nature of the processes engaged during encoding and during retrieval. Specifically, the encoding specificity (e.g. Tulving & Thompson 1973) and the transfer appropriate processing (e.g. Morris *et al.* 1977) frameworks suggest that 'only that can be retrieved that has been stored, and that how it can be retrieved depends on how it was stored' (Tulving & Thompson 1973, p. 359). Thus, for example, in most retrieval contexts, verbal experiences are more memorable when semantic and phonological attributes were attended during encoding. However, if successful retrieval depends on the encoding of orthographic or perceptual attributes of the stimulus, then conditions that foster the encoding of these attributes may result in a superior memory relative to conditions that foster the encoding of semantic and phonological attributes. Event-related fMRI methods provide a means for identifying the neural substrates that might predict subsequent memory when orthographic, perceptual, or other attributes are critical.)

In contrast to verbal encoding, non-verbal experiences may be more memorable when visuospatial attributes of the experience are extensively processed via participation of right prefrontal regions (e.g. Brewer *et al.* 1998; Kelley *et al.* 1998; Wagner *et al.* 1998*a*). Right prefrontal regions may serve to focus attention on and organize visuospatial attributes in working memory (e.g. Awh & Jonides 1998; Wagner 1999), with this information serving as an input to bilateral medial temporal regions. The findings from the event-related fMRI studies suggest that a specific experience may elicit the recruitment of frontal and MTL processes to a greater or lesser extent. The source of this variability may include differences in task demands, shifts in subjects' strategies, characteristics of the target items, or attentional modulations. Regardless of the source of this variability, greater recruitment of frontal and MTL regions will tend to produce more memorable experiences.

4. EVENT-RELATED POTENTIALS AND 'SUBSEQUENT MEMORY'

As emphasized in § 3, the recent development of event-related fMRI methods allows for identification of the neural underpinnings of various mnemonic phenomena, including those that require consideration of participant behaviour at the individual event level (such as the subsequent memory or Dm effect). Although event-related fMRI provides high spatial resolution, this method does not provide the necessary temporal resolution (at least as typically implemented) to determine the temporal sequence of cognitive processes supporting memory. For example, we speculated earlier that the temporal relationship between frontal and MTL regions during memory encoding consists of frontal regions preceding MTL regions. However, the available event-related fMRI studies do not provide data that speak to this hypothesis directly (Rugg 1998). To evaluate this hypothesis and related kinds of ideas, it will be important to integrate

these methods with others that offer higher temporal resolution, such as ERP and MEG methods. With this idea in mind, we now turn to the rich ERP literature on the Dm effect.

Over the past two decades, many researchers have attempted to gain further understanding of the cognitive and neural processes involved in human long-term memory by recording ERPs at the same time that participants engage in tasks involving memory encoding and/or memory retrieval (for general reviews, see Friedman 1992; Halgren & Smith 1987; Kutas 1988; Rugg 1995*a*,*b*). Recorded from electrodes placed on the scalp, ERPs consist of small fluctuations in the spontaneous electrical activity of the brain (electroencephalogram, or EEG) that are time locked to a particular event, such as stimulus onset. ERPs are typically described in terms of different 'components' (portions of the waveform) based on their scalp distribution (specified by electrode placement), temporal onset, and the direction of the waveform (positive-going or negative-going), as well as functional task correlates (i.e. the type of experimental manipulations that tend to evoke the component). Often, the dependent variable is either the peak or average amplitude of the waveform for a given time period, which—given the high temporal resolution of ERPs—may be separately reported for several different 'latency bands', each of a few hundred milliseconds duration or less. However, other measures, such as the latency at which the peak is observed, or the area under a given portion of the waveform, may also be used.

In this review, we adopt a relatively broad conception of the 'Dm' effect, using this term, as originally proposed by Paller *et al.* (1987*a*), to refer to any ERP difference based on later memory performance. We assume a 'non-prejudicial' stance concerning the relationship of this difference to known ERP components such as the 'P300' (a positive-going wave that is maximal at parietal and central electrode sites, with a peak latency somewhere between 300 and 600 ms post-stimulus onset, and is associated with the encoding of novel and task-relevant stimuli) or the 'N400' (a negative wave that peaks at approximately 400 ms post-stimulus onset and that is often associated with stimuli that do not 'fit' with the current context in some way). As will be further detailed below, considerable evidence suggests that it is possible to separate—at least in part—something specifically related to later memorability of items from other, independently derived, components such as the P300 and N400 (e.g. Besson & Kutas 1993; Friedman 1990*b*; Friedman & Sutton 1987; Friedman *et al.* 1996; Paller *et al.* 1987*b*; Smith 1993). For instance, Friedman & Sutton (1987) found that the Dm effect appeared to span several different components with which it overlapped, and Smith (1993) found both an earlier and later Dm component, with both a relatively early positivity (between 175 and 225 ms) and a later positivity (400–900 ms) correlating with later successful recognition. Likewise, Friedman *et al.* (1996, p. 11) suggested that the subsequent memory effect that they observed, and which spanned several ERP deflections, might be 'unitary ERP activity with a unique functional role that overlaps several ERP deflections, or it could reflect the contribution of several overlapping components, each reflecting a different function'.

Nonetheless, initial interest in the relationship of ERPs as observed during the encoding of stimuli to subsequent memory partially arose from a more specific and focused conception of the 'P300' component (Donchin 1981; Fabiani *et al.* 1985, 1990; Karis *et al.* 1984) and, especially, the role it might play in influencing 'the manner in which we respond to *future* stimuli' (Donchin 1981, p. 507, original emphasis). The P300 component is thought to reflect a form of 'updating' or 'refreshing' the contents of working memory, thereby allowing individuals to maintain an accurate, ongoing mental representation or schema of the environment (for a review, see Kutas 1988). Thus, an interest in the encoding–subsequent memory relationship, and the possibility that processing at time t should prove predictive of an individual's ability to recognize or remember an item at time $t+1$, was, in part, implied by the notion of what the initial processing 'was for'. Importantly, although several studies have reported 'subsequent memory' or 'Dm' effects that do not appear to be confined or restricted to the P300 component, this central–parietal component nonetheless often makes up an important part of the effects that are reported. Intracranial or 'depth' recordings of ERPs suggest that the P300 observed at the scalp does not originate in one place, such as the amygdala or hippocampus, but reflects contributions from several regions, including the MTL and frontal lobes (Kutas 1988).

The earliest studies that used evoked potentials to explore whether differences in the neural 'signature' observed at encoding might correlate with subsequent memory were reported nearly two decades ago. Chapman *et al.* (1978) found that the amplitude of a 'P250' component (recorded in one subject across ten sessions) appeared to act as an index to 'storage' in short-term memory inasmuch as the same items that tended to elicit the largest P250 were found—in another group of participants—to be the items that were most likely to be recalled. However, the use of measures of recall performance across rather than within participants to infer probable later memory, gives this study only 'tentative' status as a 'subsequent memory' study.

More typically cited as the first 'Dm' study is that of Sanquist *et al.* (1980). These researchers found that words that were later recognized during a 'yes or no' recognition test were accompanied—during encoding—by a larger 'late positive component' (peak latency of *ca.* 500 ms) and a less negative later-occurring slow wave component than were words that were not recognized. This difference was observed at midline electrodes in frontal (Fz), central (Cz) and parietal (Pz) sites, and was obtained with an incidental encoding task using word pairs. Specifically, for some items, participants were asked to judge if the two words in the pair rhymed, for other items they decided if the words were synonyms, and for still others they decided if the words were in the same letter case (upper or lower case). Later, they were tested for their memory of the second member of each pair. A sufficient number of trials was available only for the first two tasks (the letter case judgement task yielded especially low levels of memory), and only for a subset of participants. Consideration of these trials revealed a subsequent memory effect for three out of the four participants who had a sufficient number of rhyme judgement

trials, and three out of the three participants who had a sufficient number of trials of the synonym judgement task.

These initial results were also, however, admittedly somewhat tentative: Sanquist *et al.* (1980) could only consider results from a subset of participants for the various conditions. Further, even for the trials that were included, there was a partial confound with the nature of the encoding decision that participants reached: whereas most of the recognized items were from the 'same' encoding trials (that is, cases where the word pairs were judged to rhyme, or were similar in meaning), most of the missed (forgotten) items were from trials accompanied by a 'different' encoding judgement. It is possible that 'same' encoding trials themselves elicited a larger late positive component, independent of subsequent memory performance (cf. Karis *et al.* 1984; Neville *et al.* 1986), yet there were not enough trials to consider these conditions separately.

Fortunately, following these pioneering studies, a large number of further experiments have demonstrated the reliability and generalizability of the Dm effect. These studies have also demonstrated that charting the relationships between encoding and subsequent memorability is a complex, multi-faceted endeavour, moderated by many factors. Here we review some of these findings in relation to three central factors: (i) the nature of the stimuli (material type); (ii) the encoding or orientating tasks used; and (iii) the manner in which memory is probed during retrieval (test format).

(a) *Nature of the stimuli* (*material type*)

Numerous ERP studies have reported a 'Dm effect' when correlating the neural activity observed during the initial processing of verbal materials with later recall or recognition of those items. These studies have most often used single words—typically abstract and/or concrete nouns (Fabiani & Donchin 1995; Fabiani *et al.* 1985, 1990; Friedman 1990*b*; Friedman *et al.* 1996; Johnson *et al.* 1985; Karis *et al.* 1982, 1984; Munte *et al.* 1988; Paller 1990; Paller & Kutas 1992; Paller *et al.* 1987*a*, 1988; Rugg 1990; Smith 1993; Van Petten & Senkfor 1996; and cf. Paller *et al.* 1987*b*). Neural electrophysiological 'presages' of later successful remembering have also been found for other verbal stimuli, such as names (Fabiani *et al.* 1986), and target words initially presented in the context of sentences (Besson & Kutas 1993; Neville *et al.* 1986), or as part of a pair of words (Weyerts *et al.* 1997). As in the initial report of Sanquist *et al.* (1980), these 'subsequent memory effects' appear as a greater positivity for subsequently remembered than for subsequently forgotten items, often associated with the P300 but also extending beyond it, and distributed across central, parietal and/or frontal areas. In addition, particularly in situations where participants are explicitly instructed to attempt to remember the items, a later positive-going component in frontal areas may be observed (e.g. Friedman 1990*b*; Munte *et al.* 1988). The majority of these studies have focused on findings from electrodes placed on the midline (Fz, Cz, Pz). However, there are also instances where lateral electrodes were used, with a few of these studies suggesting that, although clearly bilateral, the subsequent memory effect for verbal materials may be somewhat left-lateralized, especially for the parietal or parieto-temporal effects (cf. Neville *et al.* 1986; Paller *et al.* 1987*a*; however, also see Paller 1990, who found a largely centralized Dm effect for cued recall, but with a marked rightward frontal shift around 450 ms).

Only a few ERP studies have examined the correlates of later successful versus unsuccessful remembering of pictorial stimuli. Friedman & Sutton (1987), using line drawings of everyday objects, reported a Dm effect in a 'continuous recognition' task paradigm. In continuous recognition, novel (new) and repeated (old) stimulus items are presented in a 'continuous' temporal stream, without a separate study or encoding phase, and the participant's task is to decide, for each item, whether it was presented earlier in the sequence or not. Friedman & Sutton (1987) tested participants' recognition of pictures in six different continuous recognition blocks, where one-third of the items in each block were 'new' and never repeated, one-third were 'new' and later repeated, and one-third were 'old'. They found a clear Dm effect, with ERPs recorded while responding to new items that were later correctly recognized (hits) more positive than ERPs to new items that were subsequently 'missed'. This effect was observed from between 100 and 200 ms post-stimulus onset until the end of the recording epoch (1700 ms) and encompassed both a parietally focused 'P300' component, which was significantly more positive, and a later (more centrally focused) negativity, which was significantly less negative, for later recognized items than for items that were missed. Because the more positive-going late negativity reached its peak after the participant's 'yes or no' recognition response had been given, this later component was interpreted as reflecting processes occurring after the item was retrieved from memory (for qualitatively similar results, see Friedman (1990*a*)).

The results of a recent study by Elger *et al.* (1997)—also using a continuous recognition task with pictures, but using recordings from intracranially placed electrodes in patients undergoing pre-surgical evaluation for temporal lobe epilepsy—concurred with the earlier study of Friedman & Sutton (1987) in demonstrating a subsequent memory effect but, in addition, showed that the effect was differently lateralized for pictures and words in the same individuals. During pre-surgical exploration, recordings (electrocorticograms and stereo-electroencephalograms) were obtained directly from the medial and lateral temporal lobes of 13 patients with right and 13 patients with left temporal lobe epilepsy (all patients showed left hemispheric language dominance). In two separate blocks, participants were shown either pictures or words; in each case, half of the items were presented only once, and half of the items were presented a second time. During the initial ('novel') presentation of both pictures and words, all patients demonstrated a negative component in the left and right anterior MTL that peaked at *ca.* 400 ms and that (at least on the non-epileptogenic side) was somewhat reduced in magnitude for the repeated presentation of items compared with their first presentation (referred to as the 'AMTL-N400'). Further, and critically from the present perspective, this effect correlated significantly with participants' subsequent correct recognition, but was lateralized by the type of material: the magnitude of the left-lateralized

AMTL-N400 correlated with later recognition of words, whereas the magnitude of the right-lateralized AMTL-N400 correlated with later recognition of pictures.

In contrast to these primarily positive findings for verbal materials, and for pictorial materials depicting everyday objects, two negative findings, or failures to find a Dm effect, have been reported for abstract or symbolic visual stimuli. Van Petten & Senkfor (1996) found no Dm effect for items that were novel abstract figures, created by five lines that joined a subset of the dots in a 3×3 grid (stimuli as used in Musen & Triesman (1990)). In this study, participants were first exposed to the novel items while judging whether or not the patterns could be drawn by continuously tracing the pattern, without lifting one's pen from the paper, and without retracing one's path. Participants were then given a 'yes or no' recognition test but, so as to ensure adequate levels of recognition, several such study–test blocks were given. Recognition of items that were judged to be 'drawable' was higher than for items that were judged to be 'non-drawable', but no subsequent memory effect was found. A failure to obtain a subsequent memory effect was also reported by Fox *et al.* (1990), using geometric symbols, and an intentional encoding task. Importantly, in both of these instances, a Dm effect was found for the same participants when the stimuli were verbal materials (either single nouns in Van Petten & Senkfor (1996), or words and consonant–vowel–consonant nonsense syllables in Fox *et al.* (1990)).

These two negative findings, particularly when considered in conjunction with the many positive findings with verbal stimuli and also the positive findings using pictures with known semantic or conceptual content (e.g. the Brewer *et al.* 1998, event-related fMRI study), are provocative, and raise the possibility that the emergence of a subsequent memory effect may—at least in some instances—depend on accessing pre-existing knowledge, or on processes wherein individuals integrate their perception and interpretation of the current stimulus with other knowledge. This was the conclusion reached by Van Petten & Senkfor (1996), and is not inconsistent with a number of further findings using verbal materials, indicating that the magnitude (or emergence) of a subsequent memory effect may be modulated by the extent to which encoding operations invoke associative or elaborative processing (e.g. Paller *et al.* 1987*a*; Weyerts *et al.* 1997; also see § 4(b)). This conclusion also meshes well with an interesting further contrast that was observed in the behavioural versus electrophysiological findings for the verbal and pattern stimuli of Van Petten & Senkfor. Behaviourally, correct recognition was significantly greater for items that were given an affirmative rather than negative encoding response. This difference was found not only for the verbal items but also for the abstract patterns. However, a Dm effect was obtained only in the case of affirmative decisions for the verbal items, with little sign of a subsequent memory effect in the other conditions. This suggests that the mere presence of a form of associative coherence or 'match' between the encoding context and the stimulus (affirmative decisions)—even when such coherence has a clear effect on later recognition accuracy—cannot be sufficient for a Dm effect to emerge.

One possibility, as noted, is that it may not simply be the amount of elaborative processing, but elaborative processing in conjunction with access to pre-existing semantic or other knowledge, that is important (for an earlier argument for a somewhat similar possibility, see Halgren & Smith (1987)). Alternatively, or in addition, there are many further factors that may account for the findings. For example, there may be greater cognitive and/or neural variability in how individuals encode abstract visual patterns than verbal stimuli, particularly if they are highly unfamiliar, or these two negative outcomes may be relatively specific to the particular stimuli and procedures used (e.g. the Fox *et al.* (1990) study involved a somewhat unusual form of testing, requiring either spatially or temporally ordered recall of the items, and the Van Petten & Senkfor paradigm involved multiple study–test cycles for patterns but not words). Nonetheless, it is clear that the question of whether a subsequent memory effect can be obtained during the encoding of abstract visual materials that are not readily translated into a verbal code merits further investigation—possibly with an experimental manipulation that systematically varies the amount and/or type of prior experience that can be brought to bear during processing of the stimulus items. If the emergence of a subsequent memory effect is partially driven by processes in which the stimulus 'meets with' pre-existing episodic or semantic knowledge, then a subsequent memory effect might emerge more clearly for abstract stimuli that were previously processed (e.g. earlier judged for their complexity, pleasantness, clarity) than for entirely novel stimuli. (Note that Van Petten & Senkfor (1996) also included a repetition manipulation in their experiment, with a small subset of items presented twice during the encoding phase. However, because these comparatively few repeated items were rarely 'missed' during recognition testing, they were not included in the analyses of the subsequent memory effect.)

(b) *Encoding or orientating tasks*

The effects of variations in the encoding operations performed on stimuli, including the extent to which specific stimuli are processed for meaning ('depth' of encoding) or are meaningfully related to other items or other knowledge that one has, have long been a focus of attention in memory research (e.g. Craik & Lockhart 1972; Craik & Tulving 1975; Einstein & Hunt 1980; Hunt & Einstein 1981). Not surprisingly, they have also formed a focus of explorations of the Dm effect, which attempts to directly map between brain activity recorded during the encoding of a specific item and that item's subsequent memorability. These studies have included both (i) direct comparisons of levels of processing during 'incidental' orientating tasks, and (ii) various comparisons of intentional encoding tasks. We discuss each of these in turn.

(i) *Direct comparisons of levels of incidental encoding*

Beginning with the early study of Sanquist *et al.* (1980), where, as noted previously, a subsequent memory effect was obtained for encoding tasks involving judgements about whether pairs of words were rhymes or were synonyms, a number of studies have directly manipulated the

type of incidental encoding task that participants performed and then examined the consequences of this encoding manipulation for the subsequent memory effect. Most of these have used what might be classified as 'item-specific' encoding tasks—that is, tasks where the participant's attention is directed to specific features or aspects of each stimulus item individually, independently of other items (Paller *et al.* 1987*a*; Paller & Kutas 1992; Friedman *et al.* 1996). In addition, a more recent study (Weyerts *et al.* 1997) involved a comparison of such an 'item-specific' task with an associative task, where encoding involves considering one or more stimulus items in relation to one another (i.e. inter-item rather than intra-item processing; cf. Mandler 1980).

Paller *et al.* (1987*a*) examined encoding and subsequent recall and recognition for words presented under one of four incidental encoding tasks, including two shallow or structural tasks ('Does the word contain exactly two vowels?' 'Are the first and last letters of the word in alphabetical order?') and two deep or semantic tasks ('Is the referent of the word a living thing?' 'Is it edible?'). Each participant performed all four types of tasks, in semi-blocked fashion. After presentation of the items, and a brief interpolated task, participants were given an unexpected free recall test for all of the items; in addition, following a further unrelated experiment, they were also given a 'yes or no' recognition test. Combining across all items, there was a clear Dm effect, with significantly greater positivity for subsequently remembered than not remembered words in the period from 400–800 ms post-stimulus onset, observed both for the recognition test and for free recall. Importantly, however, this difference in positivity was much greater for the semantic tasks than for the non-semantic tasks. Differences were also found for the affirmative versus negative nature of the encoding task (non-significantly greater Dm for affirmative encoding decisions than for negative encoding decisions; also cf. Paller *et al.* 1988). However, not all of the Dm effect could be attributed to the affirmative versus negative nature of the encoding decision because a significant Dm effect was found even when considering only items given an affirmative encoding response. In addition, although the difference in the magnitude of the Dm effect for the semantic versus non-semantic encoding tasks was clearly important, there was also a rather marked difference in the magnitude of the subsequent memory effect for the two types of semantic tasks ('edible or non-edible' greater than 'living or non-living').

Somewhat less pronounced evidence for a semantic compared with non-semantic 'Dm advantage' was obtained by Paller & Kutas (1992), using a letter judgement task for the shallow condition (count the number of times the letter 'e' appears in the word), and an image judgement task for the deep condition (decide if the referent of the word is bigger than, or smaller than, the video monitor on which the words were shown). Whereas no Dm effect was found for the shallow letter judgement task, there was a trend, from 600–800 ms post-stimulus onset, for words from the image judgement task that were later correctly recognized to show greater positivity than words that were later missed. However, this trend was found only when confining attention to words that were not successfully identified during a perceptual word identification task that was interposed between the study phase and recognition testing; words that had been re-exposed on the intervening task and that had been successfully identified in that task did not show a Dm effect. It is possible that, for these items, the further processing elicited by the intervening identification task acted to reduce the correlation between encoding during the original exposure and later memory performance (see § 4(b)(ii)).

In each of these studies, the subsequent memory effect was greater for semantically compared with non-semantically encoded items. However, the results of a study by Friedman *et al.* (1996), comparing a shallow, structural task (an alphabetic classification task, requiring participants to detect words where the first and last letters were in exact alphabetic sequence, e.g. 'moon') versus a deep, semantic task (detect words that denoted animals), showed that the Dm effect also can be observed with a shallow encoding task. Each participant received both types of orientating task in a blocked (non-intermixed) manner, with the order of the two tasks counterbalanced across participants, and with all of the items within a given task presented twice, in a new random order each time. Affirmative items comprised 20% of the items and were not tested later (i.e. only non-targets were tested). Participants were then given one of two types of test: a direct or 'explicit' stem-cued recall test requiring intentional recollection of previously studied material, or an indirect or 'implicit' stem completion task, in which participants simply provided the first words that came to mind. In each case, half of the items could be completed to form studied items and half were new (not presented) items. Participants included both younger and older adults. Older adults did not show a Dm effect in any condition (Friedman 1992, p. 55; Friedman *et al.* 1996). Importantly, younger adults showed a subsequent memory effect for both orientating tasks (slightly and non-significantly larger in the semantic than structural orientating condition). ERP responses were significantly more positive for items that were later recalled or given as completions than for non-recalled or non-completed items for recording epochs 500–700 ms, 700–900 ms and 1100–1300 ms post-stimulus onset. These differences were found for both cued recall and stem completion, but showed somewhat different spatial distributions for the two tests, tending to be maximal at the parietal site for stem completion and maximal at the Cz site for cued recall (see § 4(c)(ii)).

Last, Weyerts *et al.* (1997) compared the subsequent memory effect following a relational or associative encoding task, in which participants were asked to decide whether or not two words were semantically related to one another (e.g. cellar–roof), with a non-associative task, where participants were asked to decide whether or not they could associate the colour white with at least one of the words in the pair. During 'yes or no' recognition testing, only non-target word pairs (i.e. words that were semantically unrelated to one another, and non-associated with the colour white) were tested. Participants showed significantly greater recognition of the associatively than non-associatively encoded word pairs and a Dm effect was also obtained only for the associatively encoded pairs. This effect was seen from between 200 and 1600 ms post-stimulus onset, and was most pronounced at frontal

electrodes (right and central were non-significantly greater than left), but was also apparent at a central parietal site (see Weyerts *et al.* 1997).

Taken together, these findings suggest that the subsequent memory effect is modulated by the type of encoding task that participants perform, emerging more strongly, or more frequently, for tasks that require more extensive semantic processing than for tasks that involve a focus on structural or physical features of the stimulus items. However, these findings also indicate that engaging in semantic processing is not essential for a subsequent memory effect to emerge: a Dm effect was observed in the shallower encoding task conditions of Friedman *et al.* (1996)—although note that here the items were presented twice during encoding—as well as the rhyming task of Sanquist *et al.* (1980). Further, in both studies by Friedman *et al.* (1996) and Weyerts *et al.* (1997), a Dm effect was obtained when considering only 'negative' or 'non-target' items, indicating that the effect does not invariably depend on greater semantic processing resulting from a 'positive integration' of the stimulus with the context provided by the encoding query.

The emergence of a Dm effect in these latter (comparatively shallow) conditions may be attributable to multiple factors. Although the specific operations required by the encoding task often assume an important role, other factors deriving from specific features of particular items, or such characteristics in combination with participant factors, may also be important. In particular, although the Dm effect often appears to be associated with more extended, elaborative and relatively 'later' occurring processing, this form of processing is likely to be not entirely independent of more stimulus-driven 'attention soliciting' factors arising from the stimulus itself, and factors of the latter sort may also have an independent contribution. For example, in a study involving single words, Smith (1993) found evidence for an early 'P200' frontal-central component: from between 175 and 225 ms post-stimulus onset, subsequently remembered items showed a stronger positive-going component than subsequently forgotten items. Although this early Dm component (found where participants' task was to judge items as 'interesting' or relatively 'non-interesting') had not previously been reported, Smith (1993) pointed to a similar finding in the ERPs of Paller *et al.* (1987*a*) for words studied under semantic encoding and later tested in 'yes or no' recognition. In a footnote, Smith (1993, p. 11) speculated that 'the task correlates and frontal distribution of the effect suggest that it might be involved with the engagement of attentional or working memory resources, and that failure of such engagement has negative consequences for the subsequent memorability of stimuli'. Thus both the nature of the encoding task performed and stimulus-related factors may play a role in determining later memory.

(ii) *Intentional encoding studies*

The demonstrations of a subsequent memory effect in studies using the continuous recognition paradigm, reviewed above (Elger *et al.* 1997; Friedman & Sutton 1987; also see Friedman 1990*b*), clearly indicate that reliable Dm effects may also be observed when participants are engaged in intentional efforts to remember (and retrieve) stimuli. Additional support for this, in situations other than continuous recognition testing, has been found in several studies under conditions where participants were explicitly told to attempt to remember words for later testing (Karis *et al.* 1982; Munte *et al.* 1988; Paller 1990). Importantly, however, there are also instances where certain forms of intentional processing may preclude the emergence of a Dm effect, and/or where a stronger Dm effect may be observed for incidental encoding.

In a study directly contrasting incidental and intentional encoding within the same individuals, Munte *et al.* (1988) found a stronger Dm effect when participants performed an incidental encoding task (making a living or non-living judgement concerning presented words) than during intentional encoding, where participants were simply instructed to attempt to remember the stimuli. For the incidental encoding condition, the subsequent memory effect involved a broadly distributed positivity from 100–240 ms post-stimulus onset onwards; this peaked at about 1000 ms and was maximal at midline Cz and Pz sites. By contrast, the peak of the subsequent memory effect for the intentional encoding condition was somewhat later, and was comparatively more frontally based (maximal at Fz). Importantly, this difference for incidental versus intentional encoding was found in the initial 'familiarization' session of this multi-session study. However, because, in the familiarization session, incidental encoding always preceded intentional encoding, it is possible that participants to some extent performed both the intentional and incidental tasks during the 'intentional' task. Nonetheless, the emergence of such clear topographical and temporal differences for incidental versus intentional encoding is suggestive, especially as they were found despite the possibility of across-task contamination. Further, the observation of differing topographical and temporal patterns of the subsequent memory effect for the two conditions is broadly consistent with the findings from other studies employing intentional encoding, where a later-emerging, frontal component has also been observed (Friedman 1990*b*; Paller 1990—especially for cued recall).

Numerous more or less subtle differences may differentiate the cognitive operations engaged during incidental versus intentional encoding. However, two factors may be especially important to determining the emergence, or non-emergence, of a Dm effect. First, compared with intentional learning instructions, an incidental encoding task may yield stronger positive outcomes because it reduces both between- and within-subject variability in how the stimulus items are initially perceived, attended, evaluated, or otherwise 'processed', thereby making it easier to detect differences associated with later memorability. In some respects, continuous recognition testing could benefit from this factor, inasmuch as all participants are (minimally) attempting to perform the same task for all items (determining if they had encountered the item previously or not). Another, related, factor is that under incidental encoding instructions, participants' processing of a given stimulus is likely to be largely restricted to the time window during which that item appears, whereas intentional efforts to remember are more likely to involve 'temporally displaced' processing of the stimulus items.

Where additional, 'uncharted' processing of an item occurs at times other than that of stimulus presentation, the extent to which the specified or 'nominal' encoding episode correlates with later memory may be reduced. For example, using an intentional learning paradigm, Karis *et al.* (1984) found that the Dm effect in the P300 component for physically 'isolated' items (words that were presented in a different font size than surrounding words; see § 4(b)(iii)), tended to emerge only for participants who, during post-experimental debriefing, reported they had engaged in 'rote' rehearsal during encoding (i.e. simply silently repeating the items to themselves), but not for those who engaged in 'elaborative' rehearsal (e.g. forming images or sentences linking the items with one another). A similar outcome was observed under conditions where participants were experimentally assigned, rather than 'self-selected', to the rote versus elaborative rehearsal conditions (Fabiani *et al.* 1985, 1990). Although the participants who reported using elaborative strategies showed a normal amplitude P300 during the study phase (thus suggesting that the isolates were, indeed, perceived and processed as 'isolates'), this P300 component did not correlate with their subsequent memory performance.

These findings support the interpretation that processes associated with the P300 component are most strongly related to later memory under conditions where individuals do not subsequently engage in further (displaced) processing of the items. If further processing is not undertaken then, whatever the underlying cognitive processes that are reflected in the P300 component, they apparently continue to play an important role, and so the magnitude of the P300 correlates with later memory. Conversely, if further processing is undertaken, then the role of these earlier processes, associated with the initial perception, interpretation, and/or integration of the stimulus, is reduced. However, equally important, in these intentional learning studies is the observation of a later component—emerging at approximately 540 ms in Karis *et al.* (1984), and between 800 and 1180 ms in the Fabiani *et al.* (1990) study—that was maximal at frontal electrodes and that was greater for participants engaging in elaborative encoding than in rote encoding. Thus, neural correlates of both types of processing (rote and elaborative) in relation to subsequent memory were found, but the nature of this correlate differed depending on the individual's strategy: rote rehearsal was associated with the earlier P300, maximal in parietal and central regions, whereas elaborative rehearsal was associated with a later component, maximal in frontal regions. Although this difference in patterns was not entirely clear-cut, in that participants in the rote strategy conditions of Fabiani *et al.* (1990) also showed a frontal positive component (cf. Rugg 1995*b*), the reduced role of the P300 in contributing to the subsequent memory effect under conditions of intentional elaborative encoding appears clear.

(iii) *Contextual manipulations*

In addition to the nature of the stimulus items, and the type of processing that participants perform during encoding, a third factor—the surrounding context in which an item is initially encountered, and whether the item fits or coheres with other items, or is in some way distinctive or unusual—might also influence subsequent memory (for a review, see Fabiani & Donchin 1995; Schmidt 1985). Both context from a physical point of view (e.g. 'To what extent does the item visually "stand out" from other items or its surrounds?') and context as construed from a more conceptual or semantically-based perspective ('To what extent does the item cohere, or fit, in terms of its meaning with other items or the specific frame in which it occurs?') have been investigated.

The effects of physical isolation have been explored by Karis *et al.* (1984) and Fabiani *et al.* (1985, 1990) using a paradigm where, somewhere in the mid-portion of a sublist of words, a single word or 'isolate' is presented in a noticeably different font size from the other items. For example, in the study where they experimentally manipulated type of processing, with each participant serving in both elaborative and rote rehearsal learning conditions, Fabiani *et al.* (1990) found that participants showed a greater tendency to preferentially recall the isolated compared with non-isolated items under rote than under elaborative instructions and that the magnitude of the Dm effect as shown in the P300 component for isolate items was greater under rote than under elaborative strategy conditions. By contrast, a later Fz component (800–1180 ms post-stimulus onset) that also showed a Dm effect was somewhat more pronounced under elaborative than rote strategy conditions.

Importantly, in this study, when participants were given an unexpected memory test requiring recall of the size of the font in which the words had been shown, participants were found to be somewhat more accurate in identifying the size of isolates than non-isolate items, but this was especially true for the rote instructional condition. This outcome suggests that there may be a convergence between the neural correlates observed during encoding and later memory, not only at the level of whether or not an item was or was not remembered, but also with regard to the recollection of specific attributes of the stimulus associated with such memorability (i.e. the P300 Dm effect was greatest for isolates under rote learning, where font size was also most often recalled). This outcome also suggests that additional attempts to probe participants' recollection of particular attributes of the studied items, such as their modality, format, or location (cf. Johnson *et al.* 1993), may allow a more closely linked and analytical mapping between the nature of neural activity observed at encoding and specific forms and degrees of subsequent memorability.

Subsequent memory effects have also been examined for items that are 'isolated' in terms of their meaning or semantic attributes, rather than their physical appearance. Fabiani *et al.* (1986) explored such effects in an 'oddball' paradigm, where the stimulus items consisted either primarily of male names, or primarily of female names, and the participant's task was either to note occurrences of rare names (20% of the items) or frequent names (80% of the items). Following the 'counted names' task, participants were given an unexpected free recall test for all of the names. Counted or 'target' names were recalled significantly more often than were non-counted names, and rare names were recalled more often than frequent names. Overall, there was a significant Dm effect, such that the P300 amplitude was greater for recalled than non-recalled names; this effect was found in

all conditions, but was greater for the 'counted frequent' than the 'counted rare' condition (although, in the 'counted frequent' condition, it was the rare items that showed an especially marked positivity).

The 'counted rare' conditions of this study also yielded a second, later positivity that was also maximal at parietal and central sites. The origin of this second positivity is not clear (for a discussion, see Fabiani *et al.* 1986; Kutas 1988), but the finding seems to point both to further complexity in the relationships between the P300 (or possibly 'P300s'), contextual factors, and subsequent memory. A similar point also appears to apply to a more recent study of Fabiani & Donchin (1995), involving both 'semantic' isolates and physical isolates, and both semantic and physical orientating tasks (for both tasks, participants were also instructed to engage in rote rehearsal). In this study, the P300 component was significantly larger for recalled isolates than for non-recalled isolates, for both orientating groups and for both types of isolate; however, a subsequent memory effect was also observed in the P300 component for the control words, and there were no significant interactions involving orientating task or word type. Thus, although some findings suggest that the 'P300 Dm effect', especially under conditions of rote rehearsal, is larger for items that do not fit with other items with which they co-occur, this is not invariably the case.

Two final, highly suggestive, studies of the effects of context on the subsequent memory effect should be noted. In the first, Neville *et al.* (1986) presented target items in the context of brief phrases, where the target item either 'fit' with the context ('A type of bird. Robin.'), or did not ('A type of weapon. Sheep.'). The participant's task was to judge whether or not the word fitted with the phrase. Although a subsequent memory effect was obtained for both 'fit' and 'non-fit' items, the positive-going wave associated with the Dm effect was 'postponed' when the items did not fit with the context (positivity at *ca.* 500–550 ms) relative to when the item was congruent with the context (positivity at *ca.* 250 ms). The waveforms for the non-fit items showed a much more marked initial negativity than the fit items, reflecting the stimulus item's unexpected nature within the context of the sentence. Once 'past' the initial negativity (N400), the Dm effect was largely similar for both the fit and non-fit words.

This pattern, particularly when combined with the finding that participants showed significantly greater recognition of the fit than of the non-fit words, might be interpreted either as (i) a reflection of the detrimental mnemonic effects of 'interfering with' or possibly 'complicating' the comparatively early processing of the stimulus, or (or in addition) (ii) an indication of the detrimental mnemonic effects associated with a delayed positivity of the neural response. However, because—considering only the incongruent or non-fit words—the magnitude of the N400 peak was similar for subsequently recognized versus subsequently missed words, whereas the late positive component differentiated later remembered from not remembered items, Neville *et al.* (1986) emphasized the second factor. The 'delayed positivity' account could simultaneously explain the overall lower level of recognition of the non-fit items (they received less 'elaborative' or 'associative' processing) and coheres well with the fact that only the later positivity correlated with later recall for both the fit and non-fit items. Importantly, the absence of a correlation between the N400 component and subsequent memory parallels an outcome reported by Fabiani & Donchin (1995), using words that were 'semantic isolates' in the context of the list in which they occurred. Although such isolates elicited a large N400 component, this component did not correlate with subsequent memory whereas the P300 component clearly did (for additional data and discussion, see also Kutas (1988)).

In a related study, Besson & Kutas (1993) used target words embedded at the end of sentences. However, all of the target items made sense ('fit') in the context of the sentences. Participants were told to read the sentences for comprehension and also to attempt to remember the last words in each sentence. The items were presented repeatedly, in a study–test, study–test format: participants first studied words in the context of the sentences, then received a cued-recall test for the words where the sentence frames were the cues; thereafter, they were again shown the sentences and targets, now either in a manner identical to or different from the first presentation. The repetition manipulation involved several conditions, including two types of items (homographs and non-homographs), and with the target word, the context, or both the target word and the context changed from the first to second presentation.

Focusing initially on the results for the first presentation items, Besson & Kutas (1993) obtained a significant Dm effect, with greater positivity for subsequently recalled than non-recalled target items; this effect was found both in the 300–600 ms latency band, where the positivity difference was most prominent at Cz and Pz electrodes, and in the 600–1200 ms latency band, where it was prominent at the central and parietal midline sites and also at left and right posterior-temporal sites. Most interestingly, consideration of the magnitude of the Dm effect for the second presentation—that is, comparing ERPs during the second presentation of the sentences with whether or not they were recalled on the second cued recall test—again showed a subsequent memory effect in the 300–600 ms latency band, but the magnitude of this effect was greater for exact repetitions, with this difference found both for non-homographs compared with different context or same word items, and for homographs compared with different context or same meaning items. No such effects of context change were found for words that were not recalled. In addition, the later (600–1200 ms) Dm effect was not influenced by the context change.

The precise interpretation of these differences is not clear: did the graded nature of the Dm effect in the 300–600 ms latency range primarily reflect 'semantic' repetition effects, where identical sentences—because they had been presented previously in the exact same manner—elicited less negative responses due to their 'expected meaning', and/or does the graded effect reflect 'episodic retrieval'? In addition, the comparatively early emergence of the effect, and its overlap with the N400 latency range, appears inconsistent with the findings of Neville *et al.* (1986) and Fabiani & Donchin (1995). As suggested by Besson & Kutas (1993), the divergence from

the Neville *et al.* study might reflect stimulus differences, with the degree of incongruity implied by the sentences of the later study (all of which comprised low probability but sensible completions) having been less strong than that of the earlier study. Critically, however, the evidence that the Dm effect may be modulated in relation to prior experience, and specifically in relation to the degree of overlap with the initial study item suggests that additional studies, under conditions where items are presented repeatedly during encoding and where the degree of 'match' between the first and second presentations is varied, might provide a means of examining the effects of episodic contextual reinstatement on subsequent memory. Such tests would be particularly valuable if they involved a form of 'match–mismatch' that required less temporally extended forms of processing than required by sentences. For example, both changes in semantic meaning (e.g. different pairings of words, as in 'strawberry jam' versus 'traffic jam') and changes in the physical appearance of the item (e.g. different exemplars of a commonly labelled concept, such as 'chair', or different modalities of presentation) could be examined. Here, an experimental design without intervening testing between the first and second study presentation would allow a clearer understanding of how Dm effects might be modified by repeated encoding (see Friedman 1990*a*,*b*; Friedman *et al.* 1996; Johnson *et al.* 1985; Rugg 1990).

(iv) *Time on task—quality versus quantity of encoding*

One question of concern in the event-related fMRI study of Wagner *et al.* (1998*b*) was the possibility that subsequently remembered items were simply processed for a longer time than were items that were later forgotten. On the one hand, it is worth noting that the observation of a subsequent memory effect only under such conditions would not, of itself, be entirely without interest. Because participants were, throughout, attempting to perform one task, as accurately and quickly as they could, and the stimulus presentation was constant for all items, any differences in memorability that did emerge (regardless of whether these were further reflected in longer response times (RTs) or not) would be closely tied to the types of spontaneous variations in cognitive processing that may occur in any situation and that may correlate with later memorability. On the other hand, it is also important that Wagner *et al.* (1998*b*) were able to demonstrate that the subsequent memory effect was not entirely dependent on differences in processing duration: the Dm effect was also obtained after selecting trials to approximately equate RTs during the incidental encoding of the remembered and forgotten events, thereby indicating that emergence of the effect does not require such differences in processing time or 'duty cycle' (see also Brewer *et al.* 1998).

A similar strategy of selecting a subset of trials to match on RTs during encoding has not always been possible in ERP studies of the Dm effect, because studies have not always used an encoding task that provided specific RTs. Nonetheless, there is also some evidence that the subsequent memory effect in ERP studies does not only, or entirely, reflect differences in the duration of stimulus engagement (at least as reflected in the RTs to an encoding or orientating task). Paller *et al.* (1987*a*) found that the Dm effect did not differ for responses with RTs that were above versus below the median encoding RT, although there was a tendency for the Dm effect to be more prolonged for the slow RT condition. Friedman *et al.* (1996) obtained RTs for their semantic task that were faster than those for their structural task, thus going in the opposite direction of the magnitude of the Dm effect, which, although found for both tasks, was somewhat more pronounced for the semantic condition. Similarly, in the associative versus non-associative encoding task comparison of Weyerts *et al.* (1997), RTs to the non-associative task were reliably longer than those for the associative task, yet recognition was greater for the associative task and a subsequent memory effect was found only for the associative task. More direct evidence is provided by the words condition of Van Petten & Senkfor (1996), where a Dm effect was obtained for words given a positive (affirmative) encoding judgement. Importantly, the average RT during the encoding of subsequently recognized items in this condition (833 ms) was nearly identical to that for items that were later missed (831 ms). Together, these findings suggest that although quantity (duration) of encoding may sometimes contribute to the emergence of Dm effects, differences in the quality of encoding—however difficult these may be to assess or to concretely specify, especially on an item-by-item basis—must also play a part.

(c) *Testing format/study–test relationships*

(i) *Free recall, cued recall and recognition*

A number of studies have included two or more types of explicit test, such as free recall and recognition (Fabiani & Donchin 1995; Munte *et al.* 1988; Paller & Kutas 1992; Paller *et al.* 1987*a*, 1988), or free and cued recall (Paller 1990), thereby allowing comparisons of the magnitude and nature of the subsequent memory effect for differing retrieval formats. One of the more illuminating of these explorations was the previously described study of Fabiani & Donchin (1995), involving both physical and semantic isolates, and physical and semantic orientating tasks. These researchers found that when combining the outcomes from the immediate recall tests with that of the final recognition test—thus, designating items as both recalled and recognized, recognized only, or neither recalled nor recognized—the magnitude of the P300 responses followed an orderly progression. Specifically, the P300 amplitudes were largest for items that were both recalled and recognized, smaller for items that were recognized but not recalled, and smallest for items that were neither recalled nor recognized. This pattern was observed for the semantic and physical orientating task groups, and for isolate and non-isolate items (for an earlier report of a similar pattern but for isolates only, see Karis *et al.* (1984)). Other researchers have also found that the magnitude of the subsequent memory effect may track with the nature of the retrieval task, with a larger amplitude difference found for free recall than for recognition (Paller *et al.* 1988; Munte *et al.* 1988). Finally, Paller (1990) found that the subsequent memory effect was both smaller, and later, for cued recall than for free recall (Dm apparent from 200 ms post-stimulus onset for free recall, but primarily from 400 ms onwards for cued recall).

These findings may, in some ways, be analogous to the confidence ratings used in the event-related fMRI study of Wagner *et al.* (1998*b*), where a Dm effect was observed only in comparing 'high confidence' hits with misses, and also to those of Brewer *et al.* (1998), where neural activity associated with later recognized and 'remembered' items exceeded that found for items later recognized and designated as 'familiar'. Two (related) factors may contribute to these observations. On the one hand, the stronger Dm effects for items that are recalled or remembered on multiple tests, and for items that are either given high confidence ratings or are accorded 'remember' judgements, may arise simply because these all comprise ways of 'screening out' items that contribute noise, that is, of reducing the number of items that are 'remembered' via guessing. Alternatively, or in addition, it is also possible that items that are recalled or remembered with high confidence are recalled in part because they 'made contact with' additional knowledge or information at the time of encoding and it is this 'additional contact' that drives the Dm effect. That is, rather than simply screening out invalid or guessed items, these procedures may serve to further refine or select among items that are, indeed, remembered, but that have differing degrees of 'strength' and/or are accompanied by differing degrees of associatively related episodic information.

This second possibility is consistent with the suggestion of Paller *et al.* (1988), that sorting trials on the basis of recall rather than recognition may be more sensitive to differences in the 'encoding strength' of words. It is also consistent with a 'reverse' procedure, used by Fabiani & Donchin (1995), where they sorted the amplitude of P300 responses during encoding of physical and semantic isolates into one of three bins—trials with P300 amplitudes that exceeded the participants' mean amplitude by more than 1 s.d., trials with P300 amplitudes within 1 s.d. of the mean amplitude, and trials with P300 amplitudes that fell more than 1 s.d. below the mean amplitude—and then examined free recall and recognition accuracy associated with each of these bins. In this 'reversed matching', Fabiani & Donchin found that both free recall and recognition tended to decrease across the three bins. This conclusion also coheres nicely with the findings of Besson & Kutas (1993), discussed above, indicating a stronger subsequent memory effect for target items that re-occurred in the exact same context than for items where either the sentence context, or the target within the context sentence, was changed (suggesting a graded process rather than all-or-none). However, this conclusion fits less straightforwardly with the outcomes of a study by Smith (1993), also using the 'remember or know' judgement task but comparing 'remember or know' judgements at encoding versus test. Smith (1993) found that, although, during recognition testing, words given 'remember' judgements showed a more positive-going ERP (evident from 550–700 ms post-stimulus onset) than words given 'know' judgements, both 'remembered' and 'known' items showed a subsequent memory effect, that is, the Dm effect did not 'track' with the recollective judgement. The reason for this apparently divergent outcome is unclear. Nonetheless, it appears that the magnitude of the subsequent memory effect may often (albeit not invariably) be greater for items associated with higher levels of recall and/or recollection of associated information.

(ii) *Implicit versus explicit memory testing*

In addition to comparing the magnitude and nature of the subsequent memory effect obtained across different types of test that all require recollection, it is also possible to ask whether neural responses during encoding may prove 'predictive' of the likelihood of individuals later accessing or producing items that they had encountered previously, but where the task does not require explicit recollection of those items (although performance may be facilitated as a consequence of the earlier experience). Such indirect or 'implicit' tests of memory (Roediger & McDermott 1993; Schacter 1987) have been examined in studies by Friedman *et al.* (1996), Paller (1990), Paller & Kutas (1992) and Paller *et al.* (1987*b*). Unfortunately, across these studies, no clear agreement emerges, at least when considering only whether or not a subsequent memory effect was observed: Paller *et al.* (1987*b*) found a significant Dm effect for an implicit stem completion task but not for explicit cued recall; Friedman *et al.* (1996) found—for young adults—a significant effect for both stem-cued recall and implicit stem completion, and Paller (1990) found an effect in cued recall (and free recall) but not in implicit stem completion. Paller & Kutas (1992) found no Dm effect in an implicit perceptual word identification task. Although the reasons for the emergence or non-emergence of a Dm effect in some cases and not others are unknown (for a discussion, see Rugg 1995*b*; Paller 1990), it is notable that, in the one instance where, within a single experiment, an effect was observed on both types of test (Friedman *et al.* 1996), the effect showed a somewhat different topographical distribution for the two forms of testing, tending to be maximal at the Pz electrode site for the implicit test, but at the Cz electrode site for the explicit test. In addition, the behavioural data in this study, which included a within-subjects 'levels of processing' manipulation, provided internal evidence that participants probably did, in fact, adopt different approaches to the two tasks. Specifically, although both explicit cued recall and implicit stem completion were higher under semantic than under structural encoding, the magnitude of this 'levels of processing' difference was significantly greater for the explicit than the implicit test. Thus, the combined behavioural and neurophysiological evidence from the Friedman *et al.* (1996) study suggests that the emergence of a 'Dm' effect on the implicit test may, indeed, comprise a 'real' effect, and probably does not entirely or simply reflect 'explicit contamination', where participants convert a nominally implicit test into an explicit test (for a discussion see Schacter *et al.* 1989). Further exploration of the nature of Dm effects using event-related fMRI, under similarly ideal conditions to those used by Friedman *et al.* (1996)—that is, where the retrieval cues for the two forms of tests are identical, and where a manipulation that should dissociate performance on the two types of tests is included as part of the experimental design—would be highly informative, and could possibly provide additional evidence for differently based forms of 'encoding' that support later subsequent memory when memory is probed explicitly versus when it is probed implicitly.

5. CONCLUSIONS

This review of event-related fMRI and ERP studies of the subsequent memory effect clearly demonstrates that numerous factors may affect the neuroanatomic underpinnings and the nature of 'the Dm effect'. Factors relating to material type (words versus pictures versus abstract or symbolic materials); to the nature of the encoding or orientating task that participants adopt (different levels or types of incidental tasks, and different forms of intentional encoding, including elaborative versus rote rehearsal); to the format of the ultimate test of retention (free recall, cued recall, or recognition, as well as implicit versus explicit retrieval instructions); and to the broader context within which an item occurs (whether items are distinctive, either physically or semantically, relative to the context in which they occur, and the extent to which they do or do not reinstate the context that was present during initial encoding), all may affect not only the magnitude of the subsequent memory effect, but also (in less clearly understood ways), its temporal and topographical distribution. These many sources of variability render an observation by Van Petten & Senkfor, especially apt: 'Because the Dm is defined as the difference between subsequently remembered and forgotten items, it necessarily bears some relationship to learning. But the variability of the effect across studies indicates that the underlying cognitive processes are not fully understood and may not be unitary' (Van Petten & Senkfor 1996, p. 493). These considerations also serve to emphasize a point, noted at the outset, that references to 'the Dm effect' or 'a subsequent memory effect' primarily comprise convenient 'grouping labels', pointing to a functional commonality—the correlation of neural activity observed during earlier processing with subsequent memory performance. Yet these correlations may reflect a number of possibly quite different neural phenomena. Again, Van Petten & Senkfor state the point concisely: 'Future research may indicate that there is a *family of Dm effects* whose amplitudes and scalp distributions are intimately tied to the type of information retrieved on initial study and to the linkage of this knowledge with the current stimulus to form an episodic memory' (Van Petten & Senkfor 1996, p. 504, emphasis added). Indeed, although there have been few event-related fMRI studies of the Dm effect, results from the two available studies indicate that different neural populations subserve this effect for verbal and non-verbal materials when memory is tested using an explicit recognition measure (Brewer *et al.* 1998; Wagner *et al.* 1998*b*). Moreover, the transfer-appropriate processing and encoding specificity frameworks (Morris *et al.* 1977; Tulving & Thompson 1973) suggest that even when material type is held constant, different neural populations may subserve the Dm effect depending on the particular stimulus features that are critical for successful subsequent retrieval.

Consistent with the latter hypothesis, the outcomes of this review underscore that sharply differentiating 'encoding' from 'retrieval'—assuming that Dm is an encoding phenomenon because it involves tracking neurophysiological indices during encoding in relation to later memory performance—as far too simplistic. The nature of the subsequent memory effect cannot be accounted for without asking how memory is to be probed (e.g. free recall, cued recall, recognition; with or without explicit reference to the past learning episode; and with varying degrees of overlap or non-overlap between components present at the study and 'reinstated' at the test). Further, it is clear that even within the temporally restricted confines of the 'encoding' phase itself, 'retrieval' and 'retrieval-related' phenomena may play a role. During continuous recognition testing, both the 'encoding' of new information and attempting to remember if one has encountered an item previously are occurring together and, although to some extent temporally differentiable, probably share many features and involve many covarying factors of influence. More generally, 'semantic' and 'episodic' retrieval are clearly intimately related to—indeed partially constitutive of—processes of elaborative encoding, both when encoding focuses on individual items and when it entails inter-item associations or relational processing.

Several possible directions for further event-related studies of subsequent memory have been suggested throughout the paper. Manipulations of the amount and nature of participants' prior experience with abstract and/or pre-experimentally novel materials would allow further exploration of the important question regarding the role of previous episodic and semantic experiences in determining both the nature of the neural activity manifested during encoding and its relationship to later memorability. Further examination of the 'subsequent memory' effect in relation to explicit versus implicit testing is critical to assess whether the 'neural premonitions' of later memory performance differ depending on whether the measure of memory involves stimuli that are intentionally retrieved or involves the incidental and non-intentional use of previously acquired information in the course of some other task or activity. Investigations of the role of contextual or 'within-stimulus' reinstatement across the study and test, such as the effects of alterations in the perceptual form of items, either from study to test, or across repeated study encounters, would allow further exploration of the effects of study–test compatibility in determining the magnitude and nature of subsequent memory effects. Likewise, the incorporation of probes of more specific objective types of information about remembered items—specific features or characteristics of the items, beyond simple recall or recognition of the item itself, that could serve as additional means of sorting later memory performance—would provide increased opportunities to examine the relationships between 'what is recalled', and the extent and nature of neural activity evidenced during encoding (e.g. how the neural activity associated with items that are later recalled with particular accompanying sensory, contextual, affective, or other details differs from items that are only 'sparsely' recalled, with few such details).

Many of the above-mentioned explorations could fruitfully be pursued as either ERP or fMRI studies. However, as noted by Rugg (1998), in his commentary regarding the studies by Brewer *et al.* (1998) and Wagner *et al.* (1998*b*), the possibility of joint efforts, combining the strengths of fMRI with those of ERPs (or MEG), seems most promising. Indeed, efforts to integrate event-related methods offering high spatial resolution (millimetres

(fMRI)) with those offering high temporal resolution (milliseconds (ERP and MEG)) are essential for a more complete understanding of the neural substrates of encoding. For example, based on their event-related fMRI observations, Wagner *et al.* (1998*b*) posited a particular functional relationship between the left frontal and medial temporal regions observed to predict subsequent memory for words. As discussed earlier, it was suggested that left frontal regions mediate attention to semantic and phonological event attributes, and in so doing make available these attributes for input to medial temporal structures. To appropriately test this hypothesis, evidence regarding the temporal relationship between frontal and medial temporal components of the Dm effect is necessary.

Recently, initial efforts to integrate fMRI or PET methods with ERP or MEG methods have been reported, with these efforts consisting of constraining source localization during ERP or MEG data analysis by the fMRI or PET observations (e.g. Liu *et al.* 1998; Halgren *et al.* 1998; Heinze *et al.* 1994; Mangun *et al.* 1998). Although technical limitations complicate such efforts—for example, simultaneous recording with fMRI and MEG is impossible, thus necessitating multiple experimental sessions with a single individual or the comparison of averaged data from two different subject groups—these initial efforts have highlighted the feasibility and use of such integrative approaches. Within the context of understanding episodic encoding, such efforts should move us closer to addressing the problem we began with: why it is, even when 'much otherwise appears to be equal', we nonetheless remember some events or stimuli, whereas others fall into (at least apparent, but also possibly quite real) oblivion.

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