Fractionating Episodic Memory Retrieval using Event Related Potentials.

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1. Episodic memory supports the ability to recollect events, from remembering what one had for breakfast, to reminiscing about a friend's wedding. Traditionally, the cognitive operations that support episodic memory have been discussed with reference to one of three stages of processing; encoding, storage or retrieval (see Tulving, 1983). The cognitive operations engaged at each stage have been studied extensively, with perhaps the greatest attention having been paid to retrieval – the focus of this chapter.

According to Semon (1904, 1921), the core of episodic retrieval is an interaction between a retrieval cue and the stored record of a past experience to which the cue refers - the memory trace or engram. The interaction between cue and trace is termed *ecphory* (see Tulving, 1983; Schacter, Eich & Tulving, 1978). In this framework the cognitive operations that are engaged to bring about ecphory are distinguished from operations that mediate ecphory itself. Moreover, once ecphory has taken place the recovered episodic information may receive further processing, in order to differentiate fully its various contents. The nature of any such post-retrieval processing will be determined by the specific retrieval demands that are prevalent in a given context.

Semon's characterisation of episodic retrieval encapsulates the view that retrieval processing can be separated into those processes that are engaged in pursuit of retrieval, those that reflect retrieval itself, and those that operate on the products of retrieval (Rugg and Wilding, 2000). In this chapter we focus on studies in which these three classes of process have been investigated by using a combination of behavioural and event-related potential (ERP) measures. For the most part, we focus on the findings from studies in which ERPs were recorded while participants completed recognition memory tasks (where participants are asked to distinguish studied from unstudied stimuli), or source retrieval tasks (where participants are asked to recover contextual (or source) information from episodes). The main body of this review chapter has three sections. The first is concerned with ERP studies of the processes that are engaged in pursuit of memory retrieval. This class of processes has been investigated using ERPs only recently. Electrophysiological indices of processes that reflect or are contingent upon successful retrieval have received considerably more attention, and the second section contains a selective review of studies in which electrophysiological correlates of these two classes of process have been identified. The review in the second section provides the necessary background for the third and final section, in which we discuss how the findings from ERP studies can be related to what can be termed the 'consensus' view of the neuroanatomical basis of episodic memory (see Allan, Robb and Rugg, 2000). Before we turn to these sections, however, we provide a brief overview of the event-related potential technique, in order to orient readers who may be unfamiliar with its strengths and weaknesses (for more detailed accounts see Rugg and Coles, 1995; Picton, Lins & Scherg, 1995; Kutas and Dale, 1997).

ERPs provide a real-time record of neural activity with millisecond temporal resolution. They index changes in the neural activity that is time-locked to an *event-of-interest*, such as the presentation of a stimulus or a behavioural response (Picton, Lins & Scherg, 1995). In the majority of cognitive ERP studies, ERPs elicited on single trials are not analysed directly. Rather, all of the ERPs from the same experimental condition are averaged together (after excluding trials containing electrical artefacts). This averaging procedure is employed due to the fact that on any given trial the neural activity evoked by a stimulus is small in comparison to the level of background electrical noise. To the extent that the noise is distributed randomly on each trial, the averaging procedure will attenuate the noise while leaving unaffected that portion of the activity on each trial that has a consistent temporal relation with the stimulus event. One repercussion of reliance on averaging procedures is that ERPs can only be employed in experiments that have multiple repetitions of an event-of-interest.

Consequently, ERPs may not be an appropriate technique to employ in experiments where critical classes of events occur relatively infrequently (Rugg, 1995).

ERPs are commonly plotted as graphs that denote changes in neural activity over time. These waveform plots are characterised by a series of positive and negative deflections (peaks and troughs) that have different time courses and are prominent at different scalp locations. ERPs are typically analysed by contrasting the time courses, amplitudes and scalp distributions of ERPs that are elicited in different experimental conditions. These contrasts can reveal *quantitative* as well as *qualitative* changes in neural activity (for a fuller exposition see Rugg and Coles, 1995). Quantitative changes are manifest as differences in the amplitude (or magnitude) of ERP waveforms. They are taken to reflect variations in the degree to which the cognitive operations indexed by the waveform are engaged. Qualitative changes in neural activity are inferred from differences in the scalp distribution (the *topography*) of the ERP waveforms across conditions. Differences of this form are taken as evidence that not entirely the same brain regions, and thus not entirely the same cognitive processes, are engaged.

At this juncture it is also important to note two significant limitations that need to be borne in mind when ERPs are employed as a tool for studying neural and cognitive events. The first is that scalp-recorded ERPs have limited spatial resolution. Although information about the distribution of activity over the scalp indicates whether the same or different brain regions are engaged across experimental conditions, the intra-cerebral generators (or sources) of an ERP modulation cannot be determined unambiguously on the basis of the neural activity that is recorded at the scalp. This limitation renders ERP data less than ideal if one is interested primarily in identifying the brain regions that carry out a given cognitive operation (see Kutas and Dale, 1997). Thus, in the discussions that follow, any claims made about the generators of an ERP effect are based on converging sources of evidence (chiefly from neuropsychology).

and functional imaging), which provide additional constraints as to the likely intracerebral sources of the scalp-recorded neural activity that is acquired in ERP studies of retrieval processing.

The second important limitation of the ERP technique is that it does not sample activity from the brain uniformly. Neural activity can only be recorded from electrodes on the scalp if a number of conditions are met. If they are to give rise to detectable scalp ERP signatures, the active neurons must be organised in a (non-radially) symmetric manner, and must be activated synchronously (see Wood & Alison, 1981). Although many brain structures do not contain neurons that satisfy these conditions, clusters of neocortical pyramidal cells do. Thus, it is widely believed that the activity of such neurons is a principal source of the electrical activity that is detected at the scalp (Alison et al., 1986; Kutas and Dale, 1997). The fact that brain activity is not sampled uniformly is important because it forces a particular need for caution when interpreting the finding that equivalent ERP effects exist across two or more experimental conditions. Such a finding cannot be interpreted as reflecting identical underlying neural activity in each condition, because there may be differences in neural activity that are carried out in regions that do not produce an ERP signature which can be detected at the scalp. In light of this limitation it is prudent to make relatively conservative functional interpretations in circumstances where common ERP effects are observed across experimental conditions. With these cautionary notes in mind, we turn now to studies that have employed ERPs to investigate the neural correlates of episodic memory.

2. In this section we focus on studies of episodic retrieval processing that have been employed to investigate the processes that are engaged during an *attempt* to retrieve information from memory. The approach in these studies has been to contrast the ERPs evoked in two or more conditions where participants are assumed to have interrogated their memories in different ways. ERP modulations that differ either quantitatively or qualitatively across such conditions may reflect differences between the processes that are engaged in pursuit of retrieval in each task. It is important to note that when examined in relation to *old* (previously studied) test items any differences may also reflect the fact that what is actually retrieved will likely differ. That is, such comparisons confound processes engaged in pursuit of retrieval with those that are engaged according to what is actually retrieved (processes of the latter type are discussed in section 3). This confound can be avoided, however, as long as contrasts are made between ERPs evoked by *new* (unstudied) test items that are encountered in tasks with different retrieval requirements. By definition, ERPs evoked by new items should not index veridical episodic retrieval because no corresponding memory trace is available. Since nominally identical sets of new items can be employed in each of a pair of tasks, any differences between classes of new items likely reflect processes that are engaged in pursuit of successful retrieval (Wilding, 1999, Rugg and Wilding, 2000, for a complementary commentary, see Rugg & Henson, this volume).

Studies in which processes associated with the attempt to retrieve have been investigated have taken one of two forms. In the first of these, participants complete a single encoding task which is followed by two or more episodic retrieval tasks, each having different instructions. The assumption is that the ways in which participants interrogate their memories will vary according to the task instructions (e.g. Wilding, 1999). In the second form of task, participants complete two or more distinct encoding tasks prior to completing a single retrieval task. In this case the assumption is that the memory retrieval operations that are engaged at test will vary according to the experience of the participants at study (e.g. Rugg, Allan & Birch, 2000). Below we describe a number of studies using these approaches that have identified ERP correlates of processes engaged during retrieval attempts.

In the study of Johnson, Kounios and Nolde (1996) two groups of participants completed encoding tasks that emphasised either perceptual or semantic processing of pictures and words. In a subsequent retrieval phase an equal number of the participants completed either a recognition memory or a source memory task. The test stimuli (visually presented words) comprised an equal number of *new* words and *old* words that had been encountered either as a word at study, or as a picture that corresponded to the meaning of the written word. Standard instructions were provided for the recognition memory task; discriminate between old and new test items. For the source memory task, participants were required to distinguish old from new items, and further, to note whether words judged old had been encountered previously as a word or as a picture.

Amongst other findings, Johnson et al. (1996) showed that ERPs elicited in the source memory task were more positive-going at frontal scalp sites than were those in the recognition task. This positivity was composed of two modulations, largest at scalp electrodes located over the left and the right hemisphere, respectively. One of the effects, the rightfrontal modulation, appears to reflect processes that operate on the products of retrieval. We discuss this effect further in the next section. More relevant here is the left-sided modulation (see in particular the description of this modulation in Nolde et al., 1998), which had an earlier onset and shorter time course than it's right-sided counterpart. The authors proposed that this left frontal effect reflected the greater requirement to engage in *reflective* processing in the source memory task in comparison to the recognition task. That is, the effect appears to be modulated by the ways in which participants interrogate their memories. Unfortunately, whether the effect truly reflected processes that operate independently of retrieval success was unclear in this case, because no contrast restricted to unstudied test items was reported. ERP modulations with a similar left-frontal maximum have, however, been observed in three recent studies that have included contrasts that were restricted to classes of unstudied test items (for what may be a related effect, see Tardif, Barry, Fox and Johnstone (2000)). In the study of Ranganath and Paller (1999) each participant completed the same picture encoding task followed by two different retrieval tasks. At test, each picture took one of three forms: old, new, or new but perceptually similar to old pictures (previously presented pictures were re-scaled, resulting in small changes to their height and width). In one test condition (general retrieval), participants made old/new recognition judgements to pictures, responding *old* to previously studied pictures as well as to perceptually similar pictures. In the other test condition (specific retrieval), participants responded *old* only to previously studied pictures. These two conditions were designed to differ in the degree to which participants were required to process perceptual details of the test items.

The differences between the ERPs that were evoked by the two classes of new items were most evident over left-frontal scalp, where those from the specific retrieval condition (respond old only to studied pictures) were more positive-going from approximately 400 to 1200 ms post-stimulus (see also Ranganath and Paller, 2000). The authors reasoned that, in contrast to the general retrieval condition, the specific retrieval condition required participants to attend more closely to perceptual features of the stimuli, and to engage in more evaluative operations before making an old/new judgement. Thus, they proposed that the differences over left-frontal scalp reflected the greater demands that these informationprocessing operations imposed on attention and working memory in the pursuit of retrieval.

A recent study by Rugg, Allan & Birch (2000) also revealed differences at left-frontal scalp locations between the ERPs that were evoked by classes of unstudied test items. In this case, however, the differences were related to an encoding manipulation. Participants completed

encoding tasks in which visually presented low-frequency words were processed with respect to either their semantic or their orthographic characteristics (hereafter the *deep* and *shallow* encoding tasks, respectively). In subsequent old/new recognition blocks, each block contained words that had been processed in only one of the two encoding tasks. For unstudied items the ERPs at left-frontal scalp locations were more positive-going for the blocks that contained shallowly encoded old words. Since memory was poorer in the shallow than in the deep retrieval task, it is reasonable to assume that greater demands were placed on attention and working memory in pursuit of recognition decisions in this task. The findings are, therefore, consistent with the interpretation offered by Ranganath and Paller (1999, 2000).

The findings of Rugg et al. for written words also indicate that the left-frontal modulation is not a consequence of using picture stimuli at test, and that the differences observed by Ranganath and Paller (1999, 2000) likely do not reflect processes related to differential inspection of the surface features of test stimuli. Whilst noting that their results were consistent with a working memory-load interpretation, however, Rugg et al. (2000) also discussed an alternative account of the left-frontal effect. They observed that participants adopted different response criteria (see Snodgrass and Corwin, 1988) in the deep and shallow retrieval blocks, and that a difference in response criteria across conditions was also evident in the behavioural data from the study of Ranganath and Paller (1999). In both cases, a more stringent (conservative) criterion was adopted in the more demanding task. The left-frontal effect could therefore reflect processes related to criterion setting rather than to the differential demands placed upon working memory and/or attention (Rugg et al., 2000).

Rugg et al. (2000) also observed a second modulation that differentiated the ERPs elicited by unstudied items in the deep and shallow retrieval conditions. This effect was largest at right hemisphere centro-parietal scalp locations, and comprised a greater negativity in the ERPs

evoked by unstudied items from the deep retrieval condition. The authors suggested that this modulation likely indexes processes that are distinct from those indexed by the left-frontal effect. The principal support for this proposal was drawn from the similarity between this modulation and the N400 ERP component, a negative-going component that was identified initially in studies of language processing (Kutas and Hillyard, 1980) and is larger in tasks that require semantic rather than non-semantic processing of stimuli (see Rugg, Furda and Lorist, 1988, Chwilla, Brown and Hagoort, 1995). On the basis of this similarity, Rugg et al. (2000) proposed that participants employed retrieval strategies at test that varied according to their experiences at the time of encoding, with the N400-like modulation reflecting the greater emphasis on semantic retrieval processing in the easier of the two retrieval tasks. Whether the N400-like modulation indexes processes that are in fact distinct from those indexed by the left-frontal modulation was not clear, however, as there was no statistical evidence to support the view that the two effects were either neurally or functionally dissociable (although for recent evidence that supports the conclusions of Rugg and colleagues, see Wilding and Nobre, 2001).

The interpretations offered by Rugg et al. (2000) for these two ERP modulations are important, because they emphasise the distinction between two classes of process that can be engaged in pursuit of retrieval. The first, *retrieval effort*, refers to the differential engagement or allocation of processing resources during a retrieval attempt. One aspect of effort-related processing may be indexed by the left-frontal modulation. The functional interpretations of the left-frontal effect described above (Ranganath and Paller, 1999, 2000, and Rugg et al., 2000) illustrate two ways in which retrieval effort can be elaborated in information-processing terms. The second class of process, *retrieval orientation*, is a cognitive set that determines how memory will be interrogated (Wilding, 1999; Rugg & Wilding, 2000). That is, it determines the retrieval operations that will be engaged when a retrieval cue is

encountered. Retrieval orientation, and the processing engendered by it, will vary when participants prepare to retrieve different types of episodic information, or the same kinds of information in different ways. Rugg et al. (2000) propose that the N400-like modulation arose because participants adopted different retrieval orientations as a result of the kind of encoding operations that old items had been subjected to at study.

In summary, the studies reviewed above indicate that ERPs recorded during memory retrieval tasks index processes that operate independently of successful retrieval. This is demonstrated by the fact that reliable differences have been observed between the ERPs evoked by different classes of unstudied test items. Further studies will determine whether ERPs are in fact sensitive to processes reflecting retrieval effort as well as those that are engaged according to the retrieval orientation that participants adopt. The preceding discussion also raises the question as to how effort and orientation influence the process of retrieval itself, and in turn, the post-retrieval processing of mnemonic contents. For example, it is an open question whether orientation can determine what is eventually retrieved from memory, or whether it influences solely the way that retrieved information is processed (Rugg & Wilding, 2000; for preliminary evidence favouring the latter alternative, see Wilding and Nobre, 2001). Of course, if ERPs are to be employed in pursuit of answers to questions of this form, the essential precursor is that ERPs are in fact sensitive to episodic retrieval success. In the following section we review findings, which demonstrate that ERPs are indeed sensitive to this class of retrieval processes.

3. A class of ERP modulations called *old/new effects* index processes associated with successful episodic memory retrieval, as well as processes that operate on the products of retrieval. These effects are manifest as differences between the neural activity that is evoked by *old* and *new* test items to which accurate memory judgements have been made (see Rugg

and Allan, 1999, 2000, Johnson, 1995, Friedman and Johnson, 2000, for reviews). There is a family of old/new effects, each effect being distinguishable on the basis of its time course, scalp distribution, and sensitivity to experimental variables. We focus here on two functionally and neurally dissociable old/new effects, maximal over left-parietal and right-frontal electrode sites, respectively, which are thought to be associated with retrieval and post-retrieval processing.

The *left-parietal old/new effect* has been observed in a range of episodic retrieval tasks, including old/new recognition, cued recall and source retrieval (e.g. Smith, 1993; Paller and Kutas, 1995, Wilding and Rugg, 1996, 1997a, Allan and Rugg, 1997) and is evoked by both words and pictures (Schloerscheidt and Rugg, 1997). An example of the effect is shown in Figure 1 (see end of article). The effect comprises a positive shift in the waveforms evoked by correctly recognised old items (hits) compared to those evoked by correctly rejected new items (correct rejections). The effect typically onsets around 300-400 msec post-stimulus, lasts for 400-600 msec (although see Donaldson and Rugg, 1998, 1999, discussed below), and is largest at left temporo-parietal electrodes. Importantly, the effect is not found in the ERPs evoked by old words that are classified incorrectly as new (misses), or new words that are identified incorrectly as old (false alarms: see Allan, Wilding & Rugg, 1998). The absence of the effect for these classes of test item indicates that it does not simply reflect repetition of a stimulus, the fact that an old decision has been made, or the erroneous belief (however tentative) that an unstudied item was in fact encountered at study. In short, participants must make an accurate judgment to a studied item in order for the effect to be evoked, suggesting that the left parietal old/new effect is related specifically to processes associated with successful retrieval from episodic memory.

Discussion of the likely functional significance of the left-parietal effect has been restricted primarily to those retrieval processes that are postulated in dual process theories of recognition memory (see Mandler, 1980; Jacoby and Dallas, 1981). According to dual process theories there are two ways of arriving at an accurate recognition memory judgment – participants may be able to *recollect* having studied an item, or the item may simply be *familiar*. In operational terms, recollection permits accurate judgments of the old/new status of test items, in addition to accurate judgments concerning contextual aspects of prior encounters. Familiarity, by contrast, provides no information other than the likely old/new status of an item, and the specific mechanisms that are thought to underlie familiarity vary for different dual-process accounts (cf. Mandler, 1980 vs. Jacoby and Dallas, 1981).

In a number of ERP studies of memory retrieval the focus has been on the question of whether the left-parietal old/new effect indexes recollection or familiarity. There is now considerable evidence that the effect in fact indexes recollection (see Rugg & Allan, 1999, 2000), and that the magnitude of the effect varies according to the amount of information that is retrieved from episodic memory (Rugg, Cox, Doyle and Wells, 1995, Wilding, 2000; for discussion of a likely ERP correlate of familiarity, see Rugg, Mark, Walla, Schloerscheidt et al. 1998, Curran, 1999). The strongest evidence in support of this view has come from studies in which recollection was defined as the ability to retrieve source information accurately. For example, in one approach, participants were asked to distinguish old from new test items, and, for items judged old, to judge in which of two study contexts the item had been encountered (see in particular, Wilding and Rugg, 1996). In a related approach, participants were asked to make Remember/Know judgements (Tulving, 1985) to words they believed to be old (Smith, 1993). In these studies, the largest old/new effects were observed for the classes of old items that were associated with retrieval of contextual information, providing strong evidence for a recollection interpretation of the left-parietal old/new effect.

Further evidence consistent with this interpretation comes from two studies by Donaldson and Rugg (1998, 1999) in which recollection was defined operationally as the ability to retrieve associative information. In these studies participants were first presented with a list of semantically unrelated word pairs and asked to generate a sentence containing each pair (thereby encouraging participants to encode the specific relationship between each pair of words). Donaldson and Rugg (1998, 1999) then used either *associative recognition* or *associative recall* tests to assess memory. In associative recognition participants discriminate between test pairs that were shown in the *same* pairing at study and test and pairs that have been *rearranged* (that is, recombined into a pairing not seen at study). In associative recall participants must report the second item from a study pair when given the first item as a cue. For each task an initial old/new recognition response was required, which was followed by either a same/rearranged judgement (associative recognition) or a verbal response (associative recall). ERPs evoked by correctly rejected new stimuli were also collected in each case, providing a baseline equivalent to that employed in old/new recognition and source memory studies.

Donaldson and Rugg found that ERPs for the successful retrieval of associative information were associated with reliable left parietal old/new effects, although the effects were considerably longer lasting in the case of successful associative recognition than in recognition memory or source memory. The reason for this is unclear, and to date little research has been undertaken to investigate this issue. Regardless, in associative recall the magnitude of the left-parietal old/new effect tracks the likelihood of recollection: the effect is larger when participants recall the association than when they are unable do so. Furthermore, in associative recognition the magnitude of the left-parietal old/new effect tracks than it is for correctly recognised *rearranged* pairs, as is shown clearly in Figure 2. This second finding is particularly difficult

to reconcile with a familiarity account of the left parietal old/new effect because presumably the words are equally familiar for same and for rearranged pairs.

In the study of Wilding and Rugg already mentioned (Wilding and Rugg, 1996) a second old/new effect was observed. This effect was largest over frontal electrode sites, with a tendency to be larger over the right hemisphere than over the left. The effect onset approximately 400 msec post-stimulus and lasted for over a second. This *right-frontal old/new effect* is shown clearly in Figure 3, and has since been reported in a number of studies (see also Figure 2). The effect has been observed in conjunction with the retrieval of several different forms of information, and it has been demonstrated that the left-parietal and right-frontal effects are neurally as well as functionally dissociable (for a review see Allan, Wilding & Rugg, 1998). In contrast with the left-parietal effect, however, the functional significance of the right-frontal effect is not well established. Wilding and Rugg (1996) offered an initial functional interpretation based on the distinction between *retrieval* and *post-retrieval* processing, a distinction that was inspired initially by the dissociable memory deficits that can accompany medial-temporal lobe versus frontal lobe lesions (e.g. Moscovitch, 1992).

Given the time course and scalp distribution of the right frontal effect, as well as the fact that the effect was larger when associated with successful retrieval of study context, Wilding and Rugg proposed that the effect reflected processes that operate on the products of retrieval, and were necessary for the recovery of task-relevant contextual information. This interpretation has encountered a number of challenges, including findings that the effect is not always evident even when accurate source judgments are made (Wilding and Rugg, 1997b), and the fact that it has been observed in recognition memory tasks in which there is no explicit source retrieval requirement (Allan and Rugg, 1997, 1998, also see Rugg, Allan & Birch, 2000). Furthermore, contrary to Wilding and Rugg (1996), in some studies frontal old/new effects of equivalent magnitude have been observed across conditions in which correct recognition judgments either were or were not accompanied by accurate judgments of study context (cf. Senkfor and Van Petten, 1998, Trott, Friedman, Ritter & Fabiani, 1997, Wilding & Rugg, 1996). These disparate findings have led to proposals that the effect reflects the initiation and maintenance of retrieval search operations (Senkfor and Van Petten, 1998), or that it indexes retrieval monitoring operations (Rugg, Allan & Birch, 2000). In general, the weight of evidence favours a post-retrieval interpretation of the right-frontal old/new effect, but the details of such an interpretation remain open to question (for additional relevant comments, see Rugg & Henson, this volume).

4. In the remainder of this chapter we examine how the ERP findings discussed in the previous section relate to the predominant neuroanatomical model of episodic memory; the so-called *consensus* view of how episodic memory is carried out by the brain (Damasio, 1989; Mclelland, McNaughton and O'Reilly, 1995, Squire and Alvarez, 1995; Rubin and Greenberg, 1998). According to this view, the encoding and subsequent retrieval of episodic information necessarily involves many different neocortical regions, each specialised to process some attribute of the episode. Collectively, these neocortical regions hold the entire memory trace for that episode. The loci of the neocortical regions that store each episodic trace are determined by the content of the episode - by what the participant experiences while the episode unfolds. Critically, according to this view, a record of the regions that store each episodic trace is maintained, potentially for years, within the hippocampal region, an area to which the neocortical regions project their activity via intermediate *convergence zones* lying within multi-modal temporal neocortex (Damasio, 1989). Successful episodic retrieval involves gaining access, with a suitable retrieval cue, to the hippocampal *index* for the target episode.

It seems reasonable to view the overall aim of strategic pre-retrieval processing (discussed above), as a means of gaining access to the appropriate hippocampal index for a target episode. Once access to the trace is achieved, a cascade of neural events is held to ensue automatically (Moscovitch, 1992), culminating in the reinstatement of activity from a past episode in the neocortical regions that collectively hold the sought after episodic trace. These changes in neocortical activity are driven by the hippocampus, underlie ecphory and, furthermore, provide the information, which is used by frontally, based post-retrieval monitoring and evaluative operations. If correct at least in broad detail, this framework can be used to generate predictions about the patterns of neural activity that should be observed when different kinds of episode are retrieved, and consequently, the pattern of ERP correlates of these successful episodic retrieval operations.

Perhaps the most obvious prediction of the consensus view is that the loci of brain regions activated during retrieval should, at least partially, be determined by the nature of the perceptual and cognitive operations engaged during encoding (Allan, Robb and Rugg, 2000). Hence, the loci of brain regions activated during retrieval should change as and when different kinds of material are recollected. For example, the perceptual and cognitive operations required to process different kinds of materials, e.g. pictures versus words, would not be expected to overlap entirely. To the extent that this is the case, the recollection of verbal versus pictorial information should depend upon different brain regions.

It is particularly striking, therefore, that the nature of the encoded attribute on which source decisions are made appears to have *no* significant effect on the scalp distribution, and hence the intracerebral generators (although see caveats in section 2), of ERP old/new effects (see Allan and Rugg, 1998; Rugg and Allan, 2000). Source attributes employed in ERP studies have included speaker voice (Wilding & Rugg, 1996), surface form (pictures versus words:

Johnson et al., 1998), presentation modality (Wilding et al., 1995, Senkfor and van Petten, 1998), and temporal order (Allan and Rugg, 1998). The old/new effects in source tasks have, without exception, exhibited either one or both of the left parietal and the right frontal effects. Thus, even when source decisions are based upon the retrieval of different kinds of episodic attribute, qualitative differences in the ERP correlates of episodic retrieval operations have not been observed, counter to the predictions of the consensus view of episodic memory (although for one possible exception, see Mecklinger, 1998).

This conclusion is strengthened by the findings of two recent ERP experiments that investigated directly the consensus view described above (Allan et al., 2000). In experiment 1, Allan et al. manipulated the nature of the cognitive operations that were performed at encoding by using a depth of processing manipulation (Craik and Lockhart, 1972). This allowed two classes of study episode to be formed, termed *deep* and *shallow*. In experiment 2, different classes of study episode were formed by manipulating the sensory modality in which items were presented for study: half of the items were presented visually and half auditorally. The retrieval task in both experiments was visual word-stem cued recall. Allan et al. (2000) found that cued recall performance was substantially better for the deep than the shallowly encoded items in experiment 1. A slight but reliable cued recall advantage was also found in experiment 2 for the visual compared to the auditory study items. These differences in memory performance were accompanied by a consistent pattern of modulations for the cued recall ERP old/new effects, such that in each experiment the old/new effects were largest when evoked by stems completed with items from the more memorable class of study episode. Critically, no evidence was found in either experiment for topographic differences between the old/new effects according to the class of study episode that was recollected (see Figure 4). There were also no apparent differences in the time courses of the old/new effects according to the manner of their encoding.

The ERP experiments reported by Allan et al. (2000) failed to find evidence supporting the notion that the ecphory of different kinds of episodes is associated with the activation of different brain regions. Allan et al. suggested that their findings, in conjunction with the previous ERP literature on old/new effects, imply the existence of a core set of retrieval processes that are engaged (to different extents) whenever details of a prior episode are brought to mind successfully. Allan et al. (2000) did, however, propose an interpretation of their findings in keeping with the consensus view of episodic memory. They suggested that the neocortical processing reflected by the old/new effects might act in conjunction with the hippocampal region during retrieval, to bring about the reinstatement of activity within yet other modality- or content-specific regions of the neocortex that do not themselves generate ERP signals. Converging evidence that the medial temporal lobes, inferior frontal and inferior parietal cortices are likely locations for the generators of old/new effects associated with recognition memory comes from a study using magnetoencephalography (Tendolkar, Rugg, Fell, Vogt et al., 2000). This interpretation links the old/new effect, and in particular the early left temporo-parietally distributed component, to a binding mechanism that plays a role in reactivating neocortical traces. In other words, the old/new effects may reflect changes in the activity of the multi-modal convergence zones described above (Damasio, 1989).

This interpretation of the ERP findings is consistent with current notions regarding the potential role of convergence zones in retrieval. It appears that these regions mediate between the hippocampal region and regions of neocortex that may hold the content or modality specific features of the episodic trace (see Mesulam, 1990). If correct, it would seem reasonable to suppose that these convergence zones are among the first neocortical regions to become activated during retrieval, and that content-specific activations of episodic information may depend upon processes that take place subsequently, involving other content specific regions of the neocortex. Given the brevity of the onset time of the old/new effect, it

seems likely that it may indeed reflect an initial stage of the retrieval pathway, one that is possibly accessed prior to further modality or content specific information.

In summary, in this section we have highlighted a pattern of empirical regularities in ERP old/new effects. The intracerebral generators of these effects appear to be engaged consistently (albeit to different extents) during episodic retrieval in a wide range of tasks, despite variations in the nature of to-be-remembered materials, and variations in the perceptual and cognitive encoding operations performed upon these materials. For example, in tests employing measures of source memory, the nature of the attribute chosen as the criterial feature evidently has little effect on the loci of the brain regions activated during retrieval, at least as has so far been established to date with scalp-recorded ERPs. When considered within the framework provided by the consensus view of episodic memory, the ERP correlates of retrieval appear likely to reflect an initial stage of processing, rather than reactivation in regions that are specific to the content of retrieval.

## Summary

The findings reviewed above provide an overview of ERP studies of memory retrieval, highlighting the important distinctions that can be drawn between different stages of retrieval processing. The experiments described have revealed ERP correlates of pre-retrieval processes that form what can be broadly termed a retrieval attempt, correlates of retrieval processes themselves, and correlates of post-retrieval processes that may reflect the monitoring and evaluation of retrieved information. Given the high temporal resolution of ERP data it is perhaps not surprising that they reveal discrete stages of retrieval processing that are not only topographically and functionally dissociable, but temporally distinct as well. In this final section we discuss several questions raised by the findings reviewed above. Discussion of the ERP correlates of pre-retrieval processes associated with retrieval attempts highlights an important issue. Namely, that processes engaged in pursuit of retrieval of different types of information from memory may be separate from processes that reflect the cognitive effort that is expended during a retrieval attempt (cf. Rugg & Wilding, 2000). In all of the studies reviewed in this chapter in which putative correlates of 'pre-retrieval' processes have been identified, these two classes of process have been confounded. What is required to distinguish between these two classes of process are studies in which these two variables are controlled systematically. For example, manipulations of list length and study-test interval could be used to hold retrieval orientation constant whilst varying retrieval effort. It is an open question as to whether the differences observed in relation to retrieval orientation would remain if memory performance, as well as response bias (Rugg, Allan and Birch, 2000), were equated across conditions.

The findings in relation to ERP correlates of retrieval and post-retrieval processes are clearer. There is a wealth of evidence to suggest that the left parietal old/new effect provides an index of recollection. Available evidence, nonetheless, does not provide a *full* account of how different experimental variables influence the left parietal effect, including the exact time of onset and the duration of the effect. Episodic recollection is likely to involve search, retrieval and decision processes that operate in an iterative manner, and differentiating how these different elements can be employed flexibly may be key to specifying more completely the cognitive processes reflected by the left-parietal effect. A similar point can be made in relation to the right frontal old/new effect. It appears to be linked to post-retrieval monitoring processes, yet the specific nature of these processes, and the variables that influence them, remain unclear. Further research investigating the relationship of monitoring processes to aspects of attention and working memory may prove fruitful in this regard.

We also wish to highlight one further aspect of the findings in relation to old/new effects. In the studies discussed above the ERP old/new effects have been linked to recollection primarily on the basis of their functional characteristics. In each case however, there was no evidence for an ERP correlate of familiarity. Consequently, the data can be viewed as consistent with single process models of episodic memory, and the idea that familiarity and recollection share common functional and neural substrates. Recent evidence, however (e.g. Rugg et al., 1998; Curran, 1999; 2000), indicates that familiarity, albeit indirectly (Tsivilis, Otten and Rugg, 2001), is indexed in the electrical record, and that this index is functionally and electrophysiologically dissociable from the left-parietal old/new effect. These findings are of course consistent with the view that recognition memory depends upon at least two neurally and functionally distinct processes (Mandler, 1980; Jacoby, 1981).

A further, and perhaps more important question raised by the research reviewed here is why, despite the different orientation-related activity revealed by ERPs, the ERP correlates of episodic retrieval commonly take the form of left temporo-parietal and right frontal old/new effects. Even when participants are attempting to retrieve different contents, the same pattern of success-related old/new effects are obtained. This disparity can be seen by comparing the results from Rugg et al. (2000) and Allan, Robb and Rugg (2000), both of which employed depth of processing manipulations. Rugg et al. propose that qualitatively different processes are engaged when searching for items encoded previously under deep or shallow conditions. But in their study, as well as that of Allan et al., there is no evidence for an analogous distinction at retrieval. Why this asymmetry exists is unclear, and taken as a whole the findings to date are consistent with the possibility that processes engaged in pursuit of retrieval have little or no influence on what is in fact retrieved, at least in the paradigms employed in existing ERP studies of episodic retrieval. The relationship between these two stages of episodic retrieval processing requires elucidation.

Finally, in relation to these outstanding questions, three points are worthy of note. First, only a small number of recent ERP studies have focused on the processes that contribute to a retrieval attempt. Second, existing ERP studies of retrieval success have by no means exhausted the forms of episodic information that can be encoded and retrieved. Third, the use of dense electrode montages and the development of sophisticated data analysis techniques will continue to increase the precision with which it is possible to determine whether the same or different generators are engaged across experimental conditions. In light of these points, we are confident that ERPs will continue to provide insights into the memory-related processes that are engaged before, during and after retrieval from episodic memory.

## References

Allan, K. and Rugg, M. D. (1997). An event-related potential study of explicit memory on test of word–stem cued recall and recognition memory, Cognitive Brain Research, 4, 251-262.

Allan, K. and Rugg, M. D. (1998). Neural correlates of cued-recall with and without retrieval of source memory, Neuroreport, 9, 3463-3466.

Allan, K., Wilding, E. L. and Rugg, M. D. (1998) Electrophysiological evidence for dissociable processes contributing to recollection, Acta Psychologica, 98, 231-252.

Allan, K., Robb, W. G. K. and Rugg, M. D. (2000). The effect of encoding manipulations on neural correlates of episodic retrieval, Neuropsychologia, 38, 1188-1205.

Allison, T., Wood, C. C. and McCarthy, G. (1986). The central nervous system. In M. G. H. Coles, E., Donchin, and S. W. Porges (Eds.), Psychophysiology: systems, processes and applications. Guilford Press: London.

Chwilla, D. J., Brown, C. M. and Hagoort, P. (1995). The N400 as a function of the level of processing, Psychophysiology, 32, 274-285.

Craik, F. I. M. and Lockhart, R. S. (1972). Levels of processing: A framework for memory research, Journal of Experimental Psychology, 86, 77-82.

Curran, T. (1999). The electrophysiology of incidental and intentional retrieval: ERP old/new effects in lexical decision and recognition memory, Neuropsychologia, 37, 771-785.

Curran, T. (2000). Brain potentials of recollection and familiarity, Memory and Cognition, 28: 923-938.

Damasio, A. R. (1989). Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition, Cognition, 33, 25-62.

Donaldson, D. I. and Rugg, M. D. (1998). Recognition memory for new associations: Electrophysiological evidence for the role of recollection, Neuropsychologia, 36, 377-395.

Donaldson, D. I. and Rugg, M. D. (1999). Event-related potential studies of associative recognition and recall: Electrophysiological evidence for context dependent retrieval processes, Cognitive Brain Research, 8, 1-16.

Friedman, D., and Johnson, R.J. (2000). Event-related potential (ERP) studies of episodic memory encoding and retrieval: A selective review, Microscopy Research and Techniques, 51, 6-28.

Jacoby, L. L. and Dallas, M. (1981). On the relationship between autobiographical memory and perceptual learning, Journal of Experimental Psychology: General, 110, 306-340.

Johnson, M. K., Kounios, J. and Nolde, S. F. (1996). Electrophysiological brain activity and memory source monitoring, Neuroreport, 8, 1317-1320.

Johnson, R. (1995). Event-related potential insights into the neurobiology of memory systems. In F. Boller and J. Grafman (Eds.), Handbook of Neuropsychology, volume 9, pp. 135-164. Amsterdam: Elsevier.

Kutas, M. and Dale, A. (1997). Electrical and magnetic readings of mental functions. In M.D. Rugg (Ed.), Cognitive Neuroscience, pp. 197-242. Psychology Press.

Kutas, M. and Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity Science, 207, 203-205.

Mandler, G. (1980). Recognising: The judgement of previous occurrence, Psychological Review, 87, 252-271.

McClelland, J. L., McNaughton, B. L. and O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the success and failures of connectionist models of learning and memory, Psychological Review, 102, 419-457.

Mecklinger, A. (1998). On the modularity of recognition memory for object form and spatial location: A topographic ERP analysis, Neuropsychologia, 36, 441-460.

Mesulam, M. M. (1990). Large-scale neurocognitive networks and distributed processing for attention language and memory, Annals of Neurology, 28, 597-613.

Moscovitch, M. (1992). Memory and working-with-memory: A component process model based on modules and central systems, Journal of Cognitive Neuroscience, 4, 257-267.

Neville, H. J., Kutas, M., Chesney, C. and Schmidt, A. L. (1989). Event related brain potentials during initial encoding and recognition memory of congruous and incongruous words, Journal of Memory and Language, 25, 75-92.

Nolde, S. F., Johnson, M. K. and Raye, C. L. (1998). The role of prefrontal cortex during tests of episodic memory, Trends in Cognitive Sciences, 2, 399-406.

Paller, K. A. and Kutas, M. (1992). Brain potentials during memory retrieval provide neurophysiological support for the distinction between conscious recollection and priming, Journal of Cognitive Neuroscience, 4, 375-391. Picton, T. W., Lins, O. G. and Scherg, M. (1995). The recording and analysis of event-related potentials. In F. Boller and J. Grafman (Eds.), Handbook of Neuropsychology, volume 9, pp. 429-499. Amsterdam: Elsevier.

Ranganath, C. and Paller, K. A. (1999). Frontal brain potentials during recognition are modulated by requirements to retrieve perceptual details, Neuron, 22, 605-613.

Ranganath, C. and Paller, K. A. (2000). Neural correlates of memory retrieval and evaluation, Cognitive Brain Research, 9, 209-222.

Rubin, D. C. and Greenberg, D. L. (1998). Visual memory-deficit amnesia: A distinct amnesic presentation and etiology, Proceedings of the National Academy of Science, USA, 95, 5413-5416.

Rugg, M. D. (1995). ERP studies of Memory. In M.D. Rugg and M.G.H. Coles (Eds.),Electrophysiology of Mind: Event-Related Potentials and Cognition, pp. 132-170, Oxford:Oxford University Press.

Rugg, M. D. and Allan, K. (2000). Event-related potential studies of long-term memory. In E. Tulving and F. I. M. Craik (Eds.), The Oxford handbook of memory, pp. 521-538. Oxford: Oxford University Press.

Rugg, M. D. & Allan, K. (1999). Memory retrieval: an electrophysiological perspective. InM.S.Gazzaniga (Ed.), *The Cognitive Neurosciences, 2nd Edition* pp. 805-816. MIT Press.

Rugg, M. D., Allan, K. and Birch, C. S. (2000). Electrophysiological evidence for the modulation of retrieval orientation by depth of study processing, Journal of Cognitive Neuroscience, 12, 664-678.

Rugg, M. D., Furda, J. and Lorist, M. (1988). The effects of task on the modulation of eventrelated potentials by word repetition, Psychophysiology, 25, 55-63.

Rugg, M. D. and Wilding, E. L. (2000). Retrieval processing and episodic memory, Trends in Cognitive Sciences, 4, 108-115.

Rugg, M. D. and Coles, M. G. H. (1995). Electrophysiology of Mind. Oxford: Oxford University Press.

Rugg, M. D., Cox, C. J. C., Doyle, M. C. and Wells, T. (1995). Event-related potentials and the recollection of low and high frequency words, Neuropsychologia, 33, 471-484.

Rugg, M. D., Mark, R. E., Walla, P., Schloerscheidt, A. M., Birch, C. S. and Allan, K. (1998). Dissociation of the neural correlates of implicit and explicit memory, Nature, 392, 595-598.

Semon, R. S. (1904). The Mneme. Allen and Unwin.

Semon, R. S. (1921). Die Mneme als Erhaltendes Prinzip im Wechsel des Organischen Gesechehens. William Engelman.

Schacter, D. L., Eich, J. E. and Tulving, E. (1978). Richard Semon's theory of memory, Journal of Verbal Learning and Verbal Behavior, 17, 721-743.

Schloerscheidt, A. M. and Rugg, M. D. (1997). Recognition memory for words and pictures: an event-related potential study, Neuroreport, 8, 3281-3285.

Senkfor, A. J. and Van Petten, C. (1998). Who said what? An event-related potential investigation of source and item memory, Journal of Experimental Psychology: Learning, Memory, and Cognition, 24, 1005-25.

Smith, M. E. (1993). Neurophysiological manifestations of recollective experience during recognition memory judgements, Journal of Cognitive Neuroscience, 5, 1-13.

Snodgrass, J. G. and Corwin, J. (1988). Pragmatics of measuring recognition memory: applications to dementia and amnesia, Journal of Experimental Psychology: General, 117, 34-50.

Squire, L. R. and Alvarez, P. (1995). Retrograde amnesia and memory consolidation: A neurobiological perspective, Current Opinion in Neurobiology, 5, 169-177.

Tardif, H. P., Barry, R. J., Fox, A. M. and Johnstone, S. J. (2000). Detection of feigned recognition memory impairment using the old/new effect of the event-related potential. International Journal of Psychophysiology, 36, 1-9.

Tendolkar, I., Rugg, M. D., Fell, J., Vogt, H., Scholz, M., Hinrichs, H. and Heinze, H. J. (2000). A magnetoencephalographic study of brain activity related to recognition memory in healthy young human subjects, Neuroscience Letters, 280, 69-72.

Trott, C., Friedman, D., Ritter, W. and Fabiani, M. (1997). Item and source memory: Differential age effects revealed by event-related potentials, Neuroreport, 8, 3373-3378.

Tsivilis, D., Otten, J., and Rugg, M.D. (2001). Context effects on the neural correlates of recognition memory: an electrophysiological study, Neuron, 31, 1-20.

Tulving, E. (1983). Elements of episodic memory. Oxford: Oxford University Press.

Tulving, E. (1985). Memory and Consciousness, Canadian Psychologist, 26, 1-12.

Wilding, E. L. (1999). Separating retrieval strategies from retrieval success: An event-related potential study of source memory, Neuropsychologia, 37, 441-454.

Wilding, E. L. (2000). In what way does the parietal old/new effect index recollection?, International Journal of psychophysiology, 35, 81-87.

Wilding, E. L., Doyle, M. C. and Rugg, M. D. (1995). Recognition memory with and without retrieval of context: An event-related potential study, Neuropsychologia, 33, 743-767.

Wilding, E. L. and Rugg, M. D. (1996). An event related potential study of recognition memory with and without retrieval of source, Brain, 119, 889-905.

Wilding, E. L. and Rugg, M. D. (1997a). An event-related potential study of memory for words spoken aloud or heard, Neuropsychologia, 35, 1185-1195.

Wilding, E. L. and Rugg, M. D. (1997b). Event-related potentials and the recognition memory exclusion task, Neuropsychologia, 35, 119-128.

Wilding, E. L. and Nobre, A. C. (2001). Task-switching and memory retrieval processing: Electrophysiological evidence, Neuroreport, 16, 3613-3617.

Wood, C. C. and Allison, T. (1981). Interpretation of evoked potentials: A neurophysiological perspective, Canadian Journal of Psychology, 35, 113-135.

**Figure 1.** The 'Left-Parietal ERP old/new effect'. ERPs from left and right parietal (LP, RP) electrodes elicited by correctly classified old (hit) and new (correct rejection) words in a recognition memory test. Data from Allan and Rugg

(1997).



**Figure 2.** ERP old/new effects from left- and right- frontal and parietal (LP, RP, LF, RF) electrodes elicited by correctly classified new word pairs (correct rejections) and old word pairs that were also correctly classified according to whether the words comprising the pair had been in encountered in the same or different (rearranged) pairings when encountered at study. Data from Donaldson and Rugg (1998, Exp. 1).











**Figure 3.** Left-Parietal and Right-Frontal ERP old/new effects elicited by correctly classified new words (correct rejections) and old words that either were (hit/hit) or were not (hit/miss) assigned correctly to study context. Electrode sites as for Figure 2. Data from Wilding and Rugg (1996, Exp. 2).



**Figure 4.** Topographic voltage maps denoting the very similar scalp-distributions of the 'visual' and 'auditory' stem cued-recall ERP old/new effects over 4 post-stimulus time periods. The maps were computed for each latency window by subtracting the mean amplitude measures obtained for correct rejections from those obtained for correct stem completions, separated according to study context (visual or auditory). The greyscale bar to the right of each map indicates the mean maximum and minimum amplitudes of the effects over each time interval. Data from Allan, Robb and Rugg (2000, Exp. 2).

