

Chapter 18

Event-related potential explorations of dual processes in recognition memory

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Introduction

Most professors have plenty of first-hand experience of the distinction between recollection and familiarity. You might find yourself walking across campus and see a young woman who seems vaguely familiar as somebody you ‘know’ from somewhere, but often you are unable to recollect any detailed information about her. Is she a waitress at a favourite diner? Is she a student from a class? Which class? What was her grade? What is her name? Of course, at other times, you can recollect details about the person. This is Sophie who earned an A in my cognitive psychology class last semester, and so as she walks by you can confidently say, ‘Hi Sophie, nice work on the final exam last semester’. The distinction between recollection and familiarity is the cornerstone of dual-process theories of recognition memory (reviewed by Yonelinas 2002). In general, recollection involves the retrieval of specific details associated with something recognized, whereas familiarity can underlie recognition without the retrieval of details.

In this chapter we will review recent event-related potential (ERP) work relevant to the dual-process perspective and examine the implications of this work for understanding binding in human memory. More comprehensive reviews of ERP memory research, each addressing the dual-process perspective to some extent, are available elsewhere (Johnson 1995; Rugg 1995; Allan *et al.* 1998; Friedman and Johnson 2000; Mecklinger 2000; Wilding and Sharpe 2003). In particular, we will review evidence relevant to the hypothesis that the 300–500 ms FN400 ERP old–new effect is related to familiarity, and the 400–800 ms parietal ERP old–new effect is related to recollection.¹

ERPs recorded on the human scalp are obtained by averaging EEG activity across multiple trials designed to engage specific sensory, cognitive, or motor processes (for a methodological introduction, see Rugg and Coles (1995) and Fabiani *et al.* (2000)). By time locking the average to regularly occurring events (e.g. stimulus onset in most ERP recognition memory experiments), ERPs reflect

the activity of brain processes that are regularly associated with stimulus processing. ERPs can be differentiated by their timing (with millisecond resolution) and scalp distribution, and so different neurocognitive processes can be identified with distinct spatiotemporal voltage patterns. ERP studies of the retrieval processes associated with recognition memory have typically compared ERPs elicited by studied (old) test items with those elicited by non-studied (new) test items. Because behavioural recognition memory performance involves discrimination between old and new items, ERP differences between old and new conditions potentially reflect the activity of brain processes contributing to recognition memory.

Previous ERP studies of recognition memory have been interpreted from dual-process perspectives. ERPs recorded over parietal sites from about 400 to 800 ms following stimulus onset are more positive for old than for new stimuli (reviewed by Johnson 1995; Rugg 1995; Allan *et al.* 1998; Friedman and Johnson 2000; Mecklinger 2000; Wilding and Sharpe 2003). Previous studies suggest that this parietal old–new effect is related to recollection (reviewed by Allan *et al.* 1998; Friedman and Johnson 2000; Mecklinger 2000; Wilding and Sharpe 2003).² When subjects are asked to introspectively differentiate words specifically ‘remembered’ from those that they merely ‘know’ to be old, larger parietal old–new effects are associated with ‘remembering’ than with ‘knowing’ (Smith 1993; Düzel *et al.* 1997; Rugg *et al.* 1998b; Trott *et al.* 1999; Curran 2004; Friedman, *in press*). The parietal old–new effect is sensitive to variables believed to affect recollection more than familiarity such as level of processing (Paller and Kutas 1992; Paller *et al.* 1995; Rugg *et al.* 1995) and word–pseudoword differences (Curran 1999). The parietal old–new effect is associated with the recollection of specific information such as study modality (Wilding *et al.* 1995; Wilding and Rugg 1997b), speaker’s voice (Rugg *et al.* 1998b; Wilding and Rugg 1996, 1997a), and temporal source (Trott *et al.* 1997). More recent research, reviewed below, has upheld the hypothesized relationship between the parietal old–new effect and recollection, as well as suggesting that earlier mid-frontal ERP old–new effects may be related to familiarity.

Rugg *et al.* (1998a) were among the first to suggest that 300–500 ms mid-frontal old–new effects (here labelled ‘FN400 old–new effects’³) are related to familiarity. A level-of-processing manipulation required subjects to study words with either a semantically ‘deep’ or a semantically ‘shallow’ encoding task. The 500–800 ms parietal old–new effect was greater for correctly recognized words following deep rather than shallow encoding, but a 300–500 ms frontal old–new effect did not differentiate between shallow and deep conditions. Rugg *et al.* suggested that the 300–500 ms frontal old–new effect may be related to

familiarity because familiarity was presumed to be less sensitive than recollection to level of processing. Other evidence indicating a relationship between FN400 and familiarity was obtained in an experiment comparing recognition memory for words and pseudowords (Curran 1999). The 400–800 ms parietal old–new differences were larger for words than for pseudowords, but the 300–500 ms mid-frontal FN400 differences were similar for words and pseudowords. In addition to these old–new differences, FN400 showed a main effect of stimulus type such that it was more negative for pseudowords than for words. Thus FN400 appeared to be sensitive to both pre-experimental (pseudoword < word) and experimental (new < old) familiarity. Although the results of Rugg *et al.* (1998a) and Curran (1999) were consistent with the idea that 300–500 ms mid-frontal FN400 old–new effects are related to familiarity, these experiments did not provide particularly strong evidence because they were not originally designed to test this hypothesis.

Dissociating recollection and familiarity with study–test similarity

According to the global matching models of memory (Murdock 1982; Gillund and Shiffrin 1984; Hintzman 1988; Humphreys *et al.* 1989; Shiffrin and Steyvers 1997; Norman and O'Reilly 2003), familiarity is an assessment of the overall similarity between a test item and all study-list information in memory. Exploiting this putative property of familiarity by manipulating the similarity between studied and tested items has proved useful for dissociating familiarity from recollection. Hintzman and Curran developed a plurality recognition paradigm which provided behavioural evidence for separate recollection and familiarity processes (Hintzman *et al.* 1992; Hintzman and Curran 1994, 1995). The plurality recognition task required subjects to study plural and singular words (e.g. 'cats', 'jar') with the instruction to remember the plurality of each. The test list included studied words in their original plurality ('cats'), similar lures with reversed polarity ('jars'), and new words. The subjects were instructed to respond 'yes' for studied words, and 'no' for similar lures and new words. As expected, the false-alarm rate was much higher for similar than for new words, presumably because the similar lures were highly familiar. In several experiments items were studied a number of times (up to 20), and memory was tested with a frequency judgement test in which subjects judged how often each item was studied, but gave 'zero' estimates for similar and new words (Hintzman *et al.* 1992; Hintzman and Curran 1995). Frequency judgements increased with presentation frequency, but the false-alarm rate (frequency judgement greater than zero) to similar lures

was minimally influenced by presentation frequency. These results suggested that the familiarity of studied and similar words increased with repetition (as indexed by increasing frequency judgements), whereas the ability to recollect specific information (i.e. plurality) was barely influenced (as indexed by false alarms to similar lures).

Hintzman and Curran (1994) examined the intuitively appealing notion that familiarity should act faster than recollection (Atkinson and Juola 1973; Mandler 1980). Plurality recognition was tested with a response-deadline procedure in which subjects were forced to make recognition judgements at various randomly determined times after stimulus onset (Reed 1973; Doshier 1984; Gronlund and Ratcliff 1989; Hintzman and Curran 1997). False alarms to similar lures showed an early increase (at fast response signals) followed by a later decrease (at slow response signals). Subjects discriminated studied from new words about 420 ms after stimulus onset, but studied-similar discrimination was delayed until about 520 ms. Hintzman and Curran (1994) interpreted these results from a dual-process perspective. Fast-acting familiarity processes were sufficient for discriminating studied from new words, but familiarity exacerbated false alarms to similar lures. Slower-acting recollection processes counteracted the familiarity of similar lures, and eventually allowed subjects to discriminate between studied and similar words.

Curran (2000) sought ERP evidence for separate familiarity and recollection processes by measuring ERPs during the plurality recognition task. Analyses focused on three conditions: studied words given a 'yes' response (Studied[yes]), similar words given a 'yes' response (Similar[yes]), and new words given a 'no' response (New[no]). The Studied[yes] condition was assumed to represent accurate plurality recollection and/or familiarity (hit rate, 66 per cent). The Similar[yes] condition was assumed to represent mostly familiarity with minimal recollection of word plurality (false-alarm rate, 41 per cent). The New[no] condition was assumed to represent minimal recollection and low familiarity (correct rejection rate, 79 per cent). As predicted, the parietal old-new effect behaved as would be expected of a recollection process (Fig. 18.1(a)). Parietal amplitudes (400–800 ms) were more positive in the condition associated with high recollection (Studied[yes]) than in the conditions with low recollection (Similar[yes], New[no]). Critically, the 300–500 ms FN400 old-new effect behaved more like a familiarity-related process (Fig. 18.1(b)). The FN400 amplitude was more negative for the least familiar condition (New[no]) than the more familiar conditions (Studied[yes], Similar[yes]). Topographic analyses confirmed that the differences related to familiarity (similar[yes]—new[no]) showed a qualitatively different pattern across the scalp than differences related

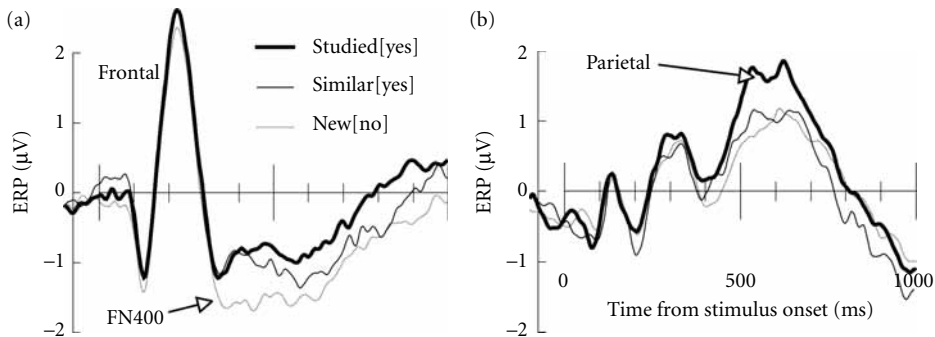


Figure 18.1 Primary results from Curran's (2000) plurality recognition experiment. (a) FN400 ERP effects hypothesized to be related to familiarity. Average ERPs from a cluster of left frontal sensors including the standard F3 location (Jasper 1958). Between 300 and 500 ms the FN400 was more negative for correctly rejected new items (New[no]) than for studied and similar items given 'yes' responses (Studied[yes], Similar[yes]). The Studied[yes] and Similar[yes] frontal ERPs did not differ between 300 and 500 ms. (b) Parietal ERP effects hypothesized to be related to recollection. Average ERPs from a cluster of left parietal sensors including the standard P3 location (Jasper 1958). Between 400 and 800 ms the parietal amplitude was more positive for the Studied[yes] than the Similar[yes] or New[no] conditions. The Similar[yes] and New[no] parietal ERPs did not differ between 400 and 800 ms.

to recollection (studied[yes]—similar[yes]) (Fig. 18.2(a)). Dissociating the two old–new effects according to the similarity manipulation, time, and topography provided strong evidence for separate familiarity and recollection processes.⁴

The impact of study–test similarity on familiarity and recollection was also found for pictures (Curran and Cleary 2003). Subjects studied grey-scale line drawings of various common objects, animals, people, and scenes, and were instructed to memorize the orientation of each. The recognition test included new pictures, identical studied pictures, and similar lures that were reversed in left–right orientation. The subjects were told to respond 'yes' only to pictures that were studied in their identical orientation, and to respond 'no' to similar (reversed orientation) lures and new pictures. Subjects were split into separate groups of 'good performers' and 'poor performers' based on their ability to discriminate between studied words and similar lures. Results from good performers replicated the plurality recognition results (Fig. 18.2(b)). The 300–500 ms FN400 effects were consistent with familiarity-related differences (New[no] < Similar[yes] = Studied[yes]) whereas the 400–800 ms parietal effects were consistent with recollection-related differences (New[no] = Similar[yes] < Studied[yes]). Poor performers showed similar FN400 familiarity effects, but 400–800 ms parietal differences showed no differentiation between studied and similar conditions (New[no] < Similar[yes] = Studied[no]).

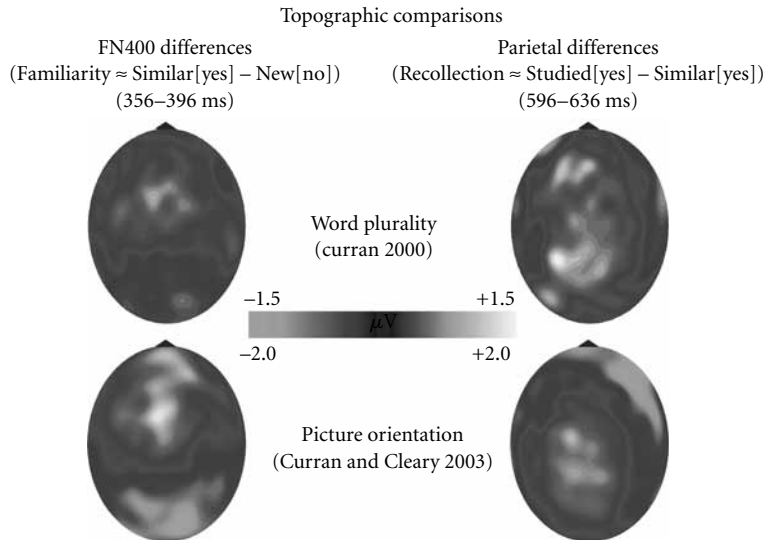


Figure 18.2 Topographical comparison of the FN400 familiarity effect with the parietal recollection effect. Each oval shows the head from above, so the nose is on top and the back of the head is on the bottom. (a) Figures from the plurality recognition experiment (Curran 2000); (b) figures from the picture orientation recognition experiment (subjects with good studied–similar discrimination only) (Curran and Cleary 2003). The figures show ERP differences between conditions that should be particularly diagnostic of familiarity and recollection processes. In each case, data are plotted within a 40 ms window occurring at the peak of each difference. In the left panels, differences between the Similar[yes] and New[no] conditions are plotted that should be primarily attributable to familiarity because recollection should be minimal in each case. The familiarity-related differences are maximal over mid-frontal regions. In the right panels, differences between the Studied[yes] and Similar[yes] conditions are plotted that should be equally familiar, but differ in recollection. The recollection-related differences are maximal over left-parietal regions.

Thus parietal recollection effects were observed only for subjects with good ability to recollect the orientation of the pictures. FN400 familiarity effects were similar regardless of the recollection ability of the subjects.

Conceptual versus perceptual influences

The role of semantic–conceptual similarity was examined using the DRM false memory paradigm (Deese 1959; Roediger and McDermott 1995). In this paradigm, a series of semantically related words are studied (e.g. candy, sour, sugar, bitter, good, tooth, etc.) that are suggestive of a non-studied theme word (‘similar lures’, e.g. sweet). Subjects tend to falsely recognize similar lures nearly as often as they correctly recognize studied words. In an ERP extension of this paradigm, subjects studied a long list of words that were divided into semantically similar

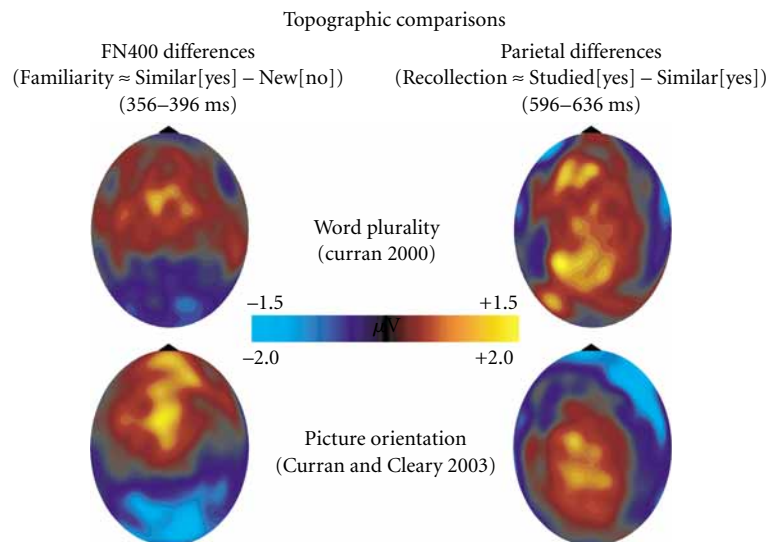


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sets (Curran *et al.* 2001). After auditory presentation of the entire study list, the subjects completed a visual recognition test that included studied words, similar lures, and new words. The subjects responded 'yes' more often to studied words (63 per cent) than to similar lures (53 per cent), and responded 'yes' more often to similar lures than to new words (23 per cent).

As in previous experiments, ERP analyses focused on three conditions: hits to studied words (Studied[yes]), false alarms to similar lures (Similar[yes]), and correctly rejected new words (New[no]). It was expected that the 300–500 ms FN400, hypothesized to index familiarity, would show a basic old–new effect, but FN400 ERPs would not differ between Studied[yes] and Similar[yes] conditions. However, no FN400 effects were observed, not even the standard old–new effect. The parietal ERP to studied words was more positive than to lures. Additionally, late frontal ERP effects (1000–1500 ms, Studied[yes] = Lure[yes] > New[no]) were larger for good than for poor performers. Similar late frontal effects have been associated with strategic retrieval and evaluation processes (Johnson *et al.* 1996; Wilding and Rugg 1997a,b; Allan *et al.* 1998; Wilding 1999; Ranganath and Paller 2000; Curran and Friedman 2003).

Although the study of false recognition in the DRM paradigm by Curran *et al.* (2001) provided evidence that late frontal processes may be important for rejecting false memories, the results did not conform to expectations regarding the hypothesized relationship of the FN400 and parietal old–new effects to familiarity and recollection. However, Nessler *et al.* (2001) found a more consistent pattern of results in a similar experiment investigating false recognition of categorically related lures. A 300–500 ms mid-frontal FN400 showed the expected familiarity pattern (New[no] < Similar[yes] = Studied[yes]), whereas 500–700 ms parietal amplitudes showed a recollection pattern (New[no] < Similar[yes] < Studied[yes]). Notably, parietal differences between similar and new conditions suggest the possibility of 'false recollection' in this experiment, which was not observed in previous ERP experiments with similar lures (Curran 2000; Curran and Cleary 2003). Nessler *et al.* further split their subjects into groups with high versus low rates of false recognition. The group with high false recognition showed no FN400 or parietal differences between studied and similar words, but both conditions differed from new (similar to subjects with poor studied–similar discrimination in Curran and Cleary (2003)). The group with low false recognition showed typical FN400 and parietal studied–new differences, but no differences between similar and new.

In a second experiment, Nessler *et al.* (2001) tested the idea that different encoding strategies may have contributed to the group differences observed in their Experiment 1. When encoding focused on the conceptual similarity of the

words, results were similar to those obtained for Experiment 1 subjects with high false-alarm rates. When encoding focused on the item-specific features, results were similar to those obtained for the Experiment 1 subjects with low false-alarm rates. Nessler and Mecklinger (2003) observed similar results in a subsequent experiment, except that FN400 similar–new differences were observed only after a short delay (40 s) and not after a long delay (80 s), as if the familiarity of lures declined across the delay. In summary, experiments by Nessler and colleagues (Nessler *et al.* 2001; Nessler and Mecklinger 2003) show that manipulating conceptual–semantic similarity leads to results very similar to manipulations of physical similarity (Curran 2000; Curran and Cleary 2003). In all cases, the 300–500 ms FN400 old–new effect is sensitive to familiarity (operationalized by differences between studied/similar, and new conditions), whereas the 400–800 ms parietal effect is sensitive to recollection (operationalized by differences between studied items and similar lures).

Evidence for 300–500 ms mid-frontal FN400 differences between new words and semantically similar lures suggests that the underlying processes are influenced by conceptual similarity (Nessler *et al.* 2001; Nessler and Mecklinger 2003). Indeed, it has been suggested that familiarity may primarily have a conceptual basis (Yonelinas 2002). However, research using novel visual objects called ‘blobs’ has suggested that FN400 old–new differences are also sensitive to perceptual similarity (Curran *et al.* 2002). Families (or categories) of blobs were created by a computer program that randomly generated a prototype and then procreated family members that were distortions of that prototype, similar to what has been done in studies of random dot classification (Posner and Keele 1968). In a training phase, subjects were shown the prototype and were asked to learn to identify a family of blobs whose members were physically similar to the prototype. Eight blobs which were in the family of the prototype were randomly intermixed with eight other blobs from outside the family, and each was presented 10 times in a task requiring subjects to categorize blobs as ‘in’ or ‘out’ of the family, with feedback. After each training set, EEG was recorded during two test lists with old and new blobs which could be either in the family or out of the family. Recognition test lists required subjects to make old–new judgements, whereas categorization test lists required subjects to make in–out judgements.

The experiment with blobs suggested that the 300–500 ms mid-frontal FN400 was sensitive to family membership as well as to recognition (Curran *et al.* 2002). FN400 was more negative to new than to old blobs, as well as being more negative to blobs outside the family than to blobs in the family. The 400–800 ms parietal effects differentiated between old and new blobs, but did not differentiate family members from non-members. Interestingly, an early (156–200 ms) N1

effect was more negative for family members than for non-members. Thus, taken as a whole, the experiment suggests a temporal transition such that earlier processes were sensitive to categorical discrimination (N1, 156–200 ms, in < out), intermediate processes were sensitive to both categorical and exemplar discrimination (FN400, 300–500 ms, in < out and new < old), and later processes were only sensitive to exemplar discrimination (parietal, 400–800 ms, old > new). The two earlier effects did not vary according to subject task (recognition versus categorization). In contrast, the parietal old–new difference was greater in the recognition than in the categorization task. The observation of task effects on parietal effects but not on FN400 effects is consistent with the perspective that recollection is particularly susceptible to intentional control, whereas familiarity is relatively automatic (Jacoby 1991; Yonelinas 2001). However, intentional retrieval may have less impact on the parietal recollection effect under less demanding conditions (Curran 1999).

Work described so far has suggested that FN400 familiarity effects are sensitive to dimensions of similarity ranging from purely perceptual (physically similar blobs (Curran *et al.* 2002)) to both perceptual and conceptual (similar words and pictures (Curran 2000; Curran and Cleary 2003)) to purely conceptual (categorically related words (Nessler *et al.* 2001; Nessler and Mecklinger 2003)). A more direct test of the relative importance of perceptual versus conceptual factors was undertaken in an experiment manipulating perceptual modality (Curran and Dien 2003). Subjects studied lists of words that were presented either visually or auditorily, and all recognition tests were visual. Both the 300–500 ms FN400 and the 400–800 ms parietal old–new effects were significant after both visual and auditory study. Thus neither effect appears to be influenced by changes in perceptual modality. Interestingly, an earlier (176–260 ms) frontal old–new difference was observed after visual but not after auditory study, and so it may be related to perceptual priming.

Challenges to the familiarity–recollection hypothesis of FN400 and parietal effects

Attention is an additional factor which may affect familiarity and recollection somewhat differently. Divided attention during study in behavioural experiments adversely affects familiarity and recollection, but affects recollection more strongly (Yonelinas 2001). Curran (2004) conducted two ERP experiments examining the effect of divided versus full attention at study on recognition of test items. Subjects studied two test lists of visually presented words. One list was studied with full attention, while the other was studied under divided attention.

To divide attention, numbers were presented auditorily and the subject pressed a button each time three consecutive odd numbers were heard. After the two study lists, the subject completed a recognition test with new words, divided attention words, and full attention words presented randomly.

Experiment 1 required subjects to discriminate between 'remembering' and 'knowing' at test (for a methodological review of the remember-know procedure see Gardiner and Richardson-Klavehn (2000)). Behavioural estimates of familiarity and recollection were both reduced by dividing attention, but divided attention had a stronger effect on recollection (replicating Yonelinas 2001). The 400–800 ms parietal ERP old–new effect was larger on trials associated with 'remembering' than with 'knowing' (replicating Smith 1993; Düzel *et al.* 1997; Rugg *et al.* 1998b; Trott *et al.* 1999), but the 300–500 ms FN400 old–new difference did not differ between 'knowing' and 'remembering'. On first consideration, one might expect the familiarity-related FN400 to be larger for 'knowing'. However, because 'knowing' is defined as the absence of 'remembering', familiarity levels for 'remember' and 'know' trials should be similar, i.e. items could be familiar regardless of whether or not they are recollected. Turning to the attention effects, the parietal old–new difference was larger after full attention during study than after divided attention, but the FN400 old–new difference was not influenced by dividing attention. This experiment appears to show an important difference between behavioural and electrophysiological indices of recollection and familiarity. Both behavioural estimates of recollection and the parietal ERP recollection effect were reduced by divided attention at study. However, the FN400 old–new difference was not influenced by divided attention, even though the behavioural estimate of familiarity was reduced.

Rather than collecting remember-know judgements at test, subjects in Experiment 2 (Curran 2004) rated their recognition responses on a four-point confidence scale (sure new, maybe new, maybe old, sure old). Words studied with full attention were recognized with greater confidence than those studied with divided attention (replicating Yonelinas 2001). Understanding how confidence influences the parietal old–new effect is important for reconciling single- and dual-process accounts of memory-related ERP effects. Some dual-process models conceptualize recollection as a high-threshold process that leads to high-confidence responses (Yonelinas 1994, 2001; Norman and O'Reilly 2003). From this perspective, conditions associated with higher recollection rates (e.g. full attention) would naturally foster higher confidence. However, from a single-process perspective that denies the existence of separate familiarity and recollection processes, confidence differences may be considered to reflect processes related more to decision-making than to memory retrieval *per se*. For example, Finnigan

et al. (2002) have promoted the idea that different ERP old–new effects can be understood as a dissociation between a single memory process and relevant decision processes (a classic signal detection perspective) rather than separate memory processes of familiarity and recollection. Finnigan *et al.* found that a 300–500 ms N400 effect recorded over the parietal scalp varied with presentation frequency, so that the effect was considered to reflect familiarity (or ‘strength’ in their terminology). A later (500–800 ms) parietal effect varied with the accuracy of recognition judgements, and so it was interpreted as being related to decision processes. Thus Finnigan *et al.* essentially supported the FN400 familiarity hypothesis but challenged the parietal recollection hypothesis, favouring the idea that parietal old–new effects are merely related to decision processes. Measuring confidence can adjudicate between the recollection and decision process account of 400–800 ms parietal effects because confidence differences attributable to recollection should only be observed for old items, whereas confidence differences arising from genetic decision processes should be observed for both old and new items.

Curran’s (2004) Experiment 2 supported the parietal recollection hypothesis, but support for the FN400 familiarity hypothesis was less clear. With regard to the recollection hypothesis, the 400–800 ms parietal ERP old–new difference was greater after full attention than after divided attention. Furthermore, confidence influenced 400–800 ms parietal amplitudes to old items but not to new items (replicating Rubin *et al.* 1999), and so the recollection hypothesis was supported over the decision-making hypothesis. With regard to 300–500 ms FN400 old–new effects, Experiment 2 (like Experiment 1) failed to find an effect of dividing attention, and so the FN400 did not respond in accord with expectations from behavioural estimates of familiarity. Curran speculated on the reasons for this null effect. First, power analyses indicated that the behavioural estimate of familiarity was more sensitive than FN400 to differences between full- and divided-attention conditions. Secondly, results from Experiment 2 suggest that confidence differences between the full- and divided-attention conditions may have obscured the influence of divided attention on FN400. Keeping in mind that confidence is higher after full attention than after divided attention, full-attention hits should be compared with high-confidence correct rejections and divided-attention hits should be compared with low-confidence correct rejections. These comparisons yielded significant FN400 old–new differences in the full-attention condition, but not in the divided-attention condition. Thus dividing attention appeared to have reduced FN400 old–new effects when confidence differences were taken into consideration.

A recent ERP study of the ‘butcher on the bus’ phenomenon raises important questions about the FN400 familiarity hypothesis (Yovel and Paller 2004).

Mandler (1980) noted that seeing familiar people in unfamiliar contexts, such as seeing your butcher on a bus, can lead to experiences of pure familiarity. Yovel and Paller (2004) studied a similar phenomenon experimentally by asking 12 subjects to study faces that were paired with verbally presented occupations. Subsequent recognition tests presented faces for old–new judgements. For faces judged old, subjects indicated whether they recollected the face’s occupation, other specifics about studying the face, or no specifics. Recollection was inferred to be associated with correct recall of the occupation or other specifics. Pure familiarity was inferred from cases in which subjects correctly recognized the faces with no specifics. According to the FN400 familiarity hypothesis, 300–500 ms frontal old–new differences should be observed between old and new faces regardless of whether or not specifics were recollected. Contrary to this prediction, the results showed no evidence of 300–500 ms frontal old–new differences between any conditions. Yovel and Paller suggested that their results provide strong evidence against the familiarity hypothesis. Furthermore, it was suggested that 300–500 ms old–new differences that others have attributed to familiarity might be understood as being related to conceptual priming (see also Olichney *et al.* 2000) because FN400 old–new differences had been typically recorded in response to words or readily nameable pictures. However, other work has shown that the 300–500 ms FN400 old–new differences can be observed with novel visual objects (the ‘blobs’ described previously (Curran *et al.* 2002)) as well as faces (Norman *et al.* 2002; Nessler *et al.* 2005; Johansson *et al.*, in press). Given other demonstrations of FN400 old–new effects with faces, Yovel and Paller’s results do not provide a very clear test of the familiarity hypothesis. A stronger test might be provided by an experiment showing typical FN400 old–new effects which did not behave in accord with familiarity, rather than demonstrating a null effect that could be attributed to innumerable experimental details. Understanding the conditions in which significant FN400 old–new effects are not observed (Curran *et al.* 2001; Yovel and Paller 2004) might further illuminate the nature of the underlying processes.

Olichney *et al.* (2000) similarly advanced the idea that 300–500 ms N400 old–new effects might be related to conceptual priming and/or short-term language comprehension processes. A mixed-aetiology group of amnesic patients completed a category verification task in which words were repeated with 0–13 intervening items. The amnesic patients showed normal 300–500 ms N400 old–new effects (comparing the first with repeated presentations), but impaired 500–800 ms parietal old–new effects. Only the parietal old–new effects were correlated with ability to recall and recognize the words later, and so the authors suggested that the N400 old–new effects might be related to conceptual

priming and/or short-term language comprehension processes rather than to episodic memory. However, subsequent work challenges this hypothesis. First, experiments demonstrating significant 300–500 ms FN400 old–new effects with ‘blobs’ and faces suggests that a completely conceptual and linguistic basis is unlikely (Curran *et al.* 2002; Norman *et al.* 2002; Nessler *et al.* 2005; Johansson *et al.*, in press). Secondly, recent work has demonstrated that 300–500 ms old–new effects can be observed when memory for pictures is tested after a 1-day retention interval, so any short-term memory account of the FN400 is unlikely to be sufficient (Curran and Friedman 2004).

Brain mechanisms of familiarity and recollection

ERPs cannot precisely localize the brain mechanisms underlying familiarity and recollection processes, but other methods have yielded some relevant evidence (reviewed by Rugg and Yonelinas 2003). When groups of amnesic patients are tested without careful screening of the aetiology or anatomical origins of their functional deficits, impairment in both familiarity and recollection (more so) have been observed in experiments using behavioural estimation techniques such as the remember–know procedure, the process dissociation procedure, or receiver operating characteristic (ROC) procedures (Yonelinas *et al.* 1998). These results suggest that both familiarity and recollection are dependent upon some subset of the structures typically damaged in amnesia, such as the hippocampus and surrounding medial temporal cortex. In general, two different possibilities could be entertained. First, recollection and familiarity might depend on the same structures such that both processes would be impaired by damage to any component structure. Alternatively, recollection and familiarity might depend upon different structures such that damaged limited to particular structures might selectively influence recollection and not familiarity, or vice versa. In general, Squire and colleagues have advanced the former view, arguing that both recollection and familiarity depend on the hippocampus and surrounding cortical regions (Manns *et al.* 2003; Stark and Squire 2003). Others have argued that recollection is specifically dependent on the hippocampus, whereas familiarity is dependent upon nearby temporal cortex (Aggleton and Brown 1999; Holdstock *et al.* 2002; Yonelinas 2002; Norman and O’Reilly 2003).

Several studies have shown that heterogenous forms of amnesia can diminish or abolish ERP old–new effects (Smith and Halgren 1989; Rugg *et al.* 1991; Mecklinger *et al.* 1998), but few studies have dissociated 300–500 ms FN400 and 400–800 ms parietal old–new effects in such patients. As mentioned previously, Olichney *et al.* (2000) found that a mixed group of amnesic patients showed normal short-term repetition effects on a 300–500 ms N400 component, but

impaired 500–800 ms parietal repetition effects. To the extent to which these short-term repetition effects recorded during a category verification task are relevant to old–new effects observed in recognition memory experiments, this experiment suggests that the two ERP old–new effects are not dependent on equivalent brain mechanisms. Other evidence relating the 400–800 ms parietal ERP old–new effect to the hippocampus (Düzel *et al.* 2001) converges with the view that hippocampal activity is central to recollection (Rugg and Yonelinas 2003). An amnesic patient with seemingly isolated bilateral hippocampal damage sustained in childhood demonstrated a typical 300–500 ms FN400 old–new effect, but the 500–700 ms parietal old–new effect was absent (Düzel *et al.* 2001). These results are consistent with functional MRI (fMRI) studies indicating that hippocampal activity is specifically associated with ‘remembering’ rather than ‘knowing’ (Eldridge *et al.* 2000) and with source recollection (Dobbins *et al.* 2003).

Other fMRI evidence suggests that recollection-related activity originating from the parietal cortex itself may contribute to the parietal ERP old–new effect. Like the parietal ERP old–new effect (Smith 1993; Düzel *et al.* 1997; Rugg *et al.* 1998b; Trott *et al.* 1999; Curran 2004; Friedman, in press), fMRI studies have found that left parietal cortex activity is greater for ‘remembering’ than for ‘knowing’ (Henson *et al.* 1999; Eldridge *et al.* 2000; Wheeler and Buckner 2004). Furthermore, the parietal ERP old–new effect (Wilding *et al.* 1995; Wilding and Rugg 1996, 1997a,b; Trott *et al.* 1997; Rugg *et al.* 1998b) and parietal fMRI activation (Cansino *et al.* 2002; Dobbins *et al.* 2003) are both associated with accurate source memory. Evidence that both the hippocampus and the parietal cortex are related to the parietal ERP old–new effect is not necessarily incompatible because recollection is likely to involve the interaction between hippocampal and cortical networks (Norman and O’Reilly 2003).

Research using other recording and imaging techniques has suggested that familiarity and 300–500 ms FN400 old–new effects may arise from the anterior temporal (possibly perirhinal) cortex. Intracranial ERP old–new effects from epileptic patients show a 400 ms peak in anterior temporal regions (AMTL–N400) (Smith *et al.* 1986; Elger *et al.* 1997; Grunwald *et al.* 1998). Old–new effects recorded with magnetoencephalography (MEG) at latencies similar to FN400 (350–450 ms) have been estimated to arise within the left, anterior, and inferior temporal regions during recognition memory tests with words (Düzel *et al.* 2003). Recent fMRI research has documented perirhinal old–new differences thought to be related to familiarity because they were sensitive to neither intention–incidental task differences nor to the amount of contextual information retrieved (Henson *et al.* 2003).

Extensions to binding

Memory binding refers to the processes by which distinct aspects of a memory are linked together to form a coherent episode. In general, binding is similar to memory processes that others have called associative (Yonelinas *et al.* 2001), chunking (Wicklegren 1979), configural (Rudy and Sutherland 1994), conjunctive (O'Reilly and Rudy 2001), or relational (Eichenbaum and Cohen 2001). Although theoretical details differ among these authors, they all generally agree that the hippocampus and/or medial temporal cortex play an important role in memory binding. From a broader perspective, other memory phenomena requiring some type of binding include source recognition and context effects. For successful source recognition, information about the item must be bound to its source. Context effects are observed when item memory benefits from matching rather than mismatching study–test context (Godden and Baddeley 1980), and this requires some binding between item and context.

From a dual-process perspective, it has been claimed that familiarity is sufficient to support recognition of single items, yet recollection is necessary for associative recognition involving pairs of items (Yonelinas 1997, 1999; Hockley and Consoli 1999; Westerman 2001; Macken 2002). Indeed, much of the research supporting the recollection hypothesis of the 400–800 ms parietal ERP old–new effects can be conceptualized as requiring binding. When subjects are asked to recollect the modality (Wilding *et al.* 1995; Wilding and Rugg 1997b), speaker's voice (Rugg *et al.* 1998b; Wilding and Rugg 1996, 1997a), or temporal source (Trott *et al.* 1997) of studied words, the judgement requires binding between the words and these specific attributes. In all cases, the 400–800 ms parietal ERP old–new effect has been shown to depend upon recollection of these bound attributes. More direct evidence comes from studies of associative recognition in which subjects study pairs of words (e.g. table–shoe, pizza–cat, car–hammer) followed by associative recognition tests requiring discrimination between same pairs (table–shoe), rearranged pairs (pizza–hammer), and new pairs (pencil–lake). A 600–900 ms parietal ERP old–new effect is larger for correctly classified same pairs than for rearranged pairs (Donaldson and Rugg 1998 1999).

A more contentious issue is whether or not familiarity can involve binding. Familiarity has sometimes been described as contextually insensitive (Atkinson and Juola 1974; Mandler 1980; Perfect *et al.* 1996; Tsivilis *et al.* 2001; Finnigan *et al.* 2002; Macken 2002), implying that item–context binding does not contribute to familiarity. Similarly, it has been suggested that associative recognition is influenced more by recollection than by familiarity (Yonelinas 1997; Rotello and Heit 2000). Although it may be true that familiarity is incapable of directly

retrieving information about associated details such as source or context, nonetheless binding processes that link items together with associated information may contribute to the computation of familiarity. If we assume that the processes underlying familiarity operate similarly to the global matching models of memory, then it should be expected that familiarity is sensitive to contextual–associative variation. Although the associative–contextual mechanisms built into the global matching models have had difficulty accounting for detailed aspects of the empirical results and these difficulties have led some to favour dual-process accounts (reviewed by Clark and Gronlund 1996), it remains possible that familiarity is contextually–associatively sensitive. In general, according to the global matching perspective as well as the encoding specificity principle (Tulving and Thomson 1973), if items are encoded along with contextual–associative information, and contextual–associative information available at test is used to probe memory along with the test item, then familiarity should show contextual–associative effects. Indeed, the bind cue decided model of episodic memory (BCDMEM) suggests that the binding of items, contexts, and other information plays a central role in the computation of familiarity (Dennis and Humphreys 2001). A recent review found that the predictions made by global matching models are generally consistent with the pattern of effects found in environmental context-dependent memory (Smith and Vela 2001). The global matching models can also be extended to provide a more detailed account of context effects (Murnane *et al.* 1999). In summary, in principle there are reasons to believe that some form of binding may contribute to familiarity.

Tsivilis *et al.* (2001) have recently published an ERP experiment directly relevant to binding. Participants studied pictures of objects (e.g. radio, lantern, envelope) superimposed on unrelated scenes (e.g. lakes, mountains, valleys). A later recognition test specifically tested subjects' memory for the objects, but incidentally manipulated the background context. The object–context pairs were arranged into five conditions: same (studied object paired with studied scene), rearranged (studied object paired with a different studied scene), old–new (studied object paired with an unstudied scene), new–old (unstudied object paired with a studied scene), and new–new (both unstudied object and scene). When both parts (object and context) of the display were present at study and test (same and rearranged), the 300–500 ms FN400 differed from conditions in which the object and/or the context were new (old–new, new–old, new–new). The 700–900 ms parietal old–new effect differentiated between conditions associated with hits (same, rearranged, old–new) and those associated with correct rejection (new–old, new–new), regardless of the contextual manipulation. Regarding the notion of 'binding', comparing the same and rearranged conditions

is critical because these conditions were equated for object familiarity and context familiarity. Differences between the same and rearranged conditions would indicate that the underlying memory processes are sensitive to the binding between objects and contexts. Tsivilis *et al.* did not observe any differences between the same and rearranged conditions, and so no evidence for binding was obtained.

One limitation of the study by Tsivilis *et al.* (2001) is that objects and contexts were not completely counterbalanced across the five conditions, and so the results may have been influenced by item effects. We recently replicated Tsivilis *et al.*'s experiment, but ensured complete counterbalancing of objects–contexts across subjects (Piatt, Curran, Collins, and Woroch, unpublished data). Only results from the same, rearranged, and new–new conditions are presented here because they are most pertinent to binding. Subjects were significantly more accurate in the same (83 per cent) as in the rearranged (78 per cent) conditions, and so their performance was sensitive to object–context binding. The new–new condition was more accurate (89 per cent) than either of the former conditions. The primary ERP results are shown in Figure 18.3. Condition (same, rearranged, new–new) \times hemisphere analyses of variance (ANOVAs) were run on the 300–500 FN400 effects recorded over frontal regions (electrode clusters around F3 and F4) (Jasper 1958) and on the 400–800 ms parietal effects over parietal regions (electrode clusters around P3 and P4) (Jasper 1958). Condition effects were significant for both components: FN400, $F(2, 29) = 10.07$, $MSE = 2.23$, $P < 0.001$; parietal, $F(2, 29) = 6.04$, $MSE = 2.57$, $P < .01$. Critically, the difference between same and the rearranged conditions was significant for FN400 ($F(2, 29) = 6.97$, $MSE = 2.23$, $P = 0.01$) and marginally significant for

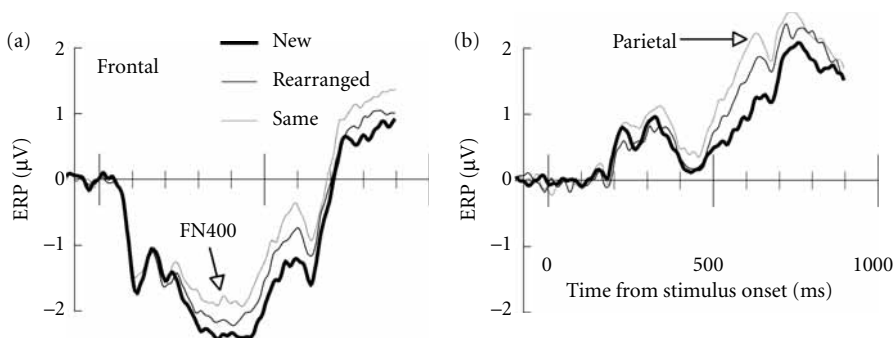


Figure 18.3 Primary results from Piatt, Curran, Collins, and Woroch (unpublished data). ERPs were computed from correct trials only. (a) Average ERPs from a cluster of left frontal sensors including the standard F3 location (Jasper 1958). (b) Average ERPs from a cluster of left parietal sensors including the standard P3 location (Jasper 1958).

the parietal effects ($F(2, 29) = 3.94$, $MSE = 2.57$, $P = 0.06$). These results suggest that, given the assumption that FN400 is related to familiarity, familiarity was sensitive to the binding of objects with contexts.

More work is needed to explore further the extent to which binding may influence the ERP correlates of recognition memory. For example, Donaldson and Rugg (1998, 1999) have observed 600–900 ms parietal ERP differences between same and rearranged conditions in experiments with word pairs, but did not report early differences that might be related to FN400. Another recent study with same, rearranged, and new word pairs reported widespread 300–600 ms same–rearranged differences (Van Petten *et al.* 2002). Although Van Petten *et al.* interpret their 300–600 ms results as replicating Donaldson and Rugg's (1998, 1999) 600–900 ms results, the temporal offset of these effects raises the question of whether their effects are more related to the 300–500 ms FN400 effects or the 400–800 ms parietal effects. Some have argued that associative effects on familiarity will occur to the extent to which the information to be associated can be encoded as a single unitized representation (Murnane *et al.* 1999; Yonelinas *et al.* 1999). It seems likely that the procedure of combining objects and contexts used by Tsivilis *et al.* (2001) is likely to foster more unitization than unrelated words, so this could explain why we were able to observe significant 300–500 ms FN400 same–rearranged differences with this method. Furthermore, subjects were specifically instructed to reject rearranged pairs in the associative recognition studies with words, whereas rearranged object–context pairs should be given 'yes' responses in the method of Tsivilis *et al.* because judgements were based on objects alone, regardless of context. Further research will be needed to test the relevance of these various factors, but the results of Piatt *et al.* (unpublished) clearly establish an influence of binding under the particular conditions of that experiment.

Binding may play a more important role in recollection than familiarity, but it may be overly simplistic to suggest that it influences only the former process. Norman and O'Reilly (2003) have developed a biologically plausible dual-process model suggesting that the hippocampus primarily contributes to recollection whereas adjacent cortical regions contribute to familiarity. Both the hippocampal recollection network and the cortical familiarity network support binding, but they do so in different ways. Familiarity may involve low-order cortical binding by conjoining only a small number of features, whereas recollection may benefit from higher-order binding within the hippocampus (O'Reilly *et al.* 2003). If, as we have argued, distinct ERP components are associated with recollection and familiarity, future ERP research may be useful for testing such theoretical perspectives on binding.

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Notes

1. In addition to the 300–800 ms ERP old–new effects that are the focus of this review, late (roughly 800–1500 ms) right frontal ERP old–new effects are often observed. Their precise functional significance is unclear, but they are often associated with some sort of post-retrieval evaluation processes (reviewed by Allan *et al.* 1998; Friedman and Johnson 2000; Rugg and Allan 2000; Wilding and Sharpe 2003).
2. The 400–800 ms parietal ERP old–new effect co-occurs with the P300 component (Bentin and McCarthy 1994; Spencer *et al.* 2000), and has been variously labelled the P300 old–new difference (Johnson 1995), the late ERP old–new effect (Rugg 1995), the P600 old–new effect (Rugg and Doyle 1992; Curran 1999), and the late positive complex (LPC) (Olichney *et al.* 2000) old–new effect.
3. The 300–500 ms FN400 old–new effect has elsewhere been called the mid-frontal (Tsivilis *et al.* 2001), medial frontal (Friedman and Johnson 2000), or early frontal (Mecklinger 2000) old–new effect.
4. We have measured EEG with a 128-channel geodesic sensor net (Tucker 1993) and used an average-reference transformation to analyse ERPs (Curran *et al.* 1993; Dien 1998). With respect to the mastoid reference that is often used in ERP studies of memory, old–new effects are usually characterized by more positive amplitudes for old than for new items over superior regions of the scalp. With respect to the average reference, we typically find that the superior old > new differences are accompanied by inferior differences of opposite polarity (new < old), as can be seen in Figure 18.2. Thus, when both superior and inferior regions are analysed, old–new effects are characterized by old–new \times superior–inferior interactions. These interactions have been the focus of our earlier work, but we have generally found the superior aspects more reliable. Thus, for simplicity and comparability with mastoid reference results from other laboratories, we primarily focus on the superior effects in this review.

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