BRAIN RESEARCH 1455 (2012) 90–102

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Research Report

Event-related potential evidence for separable automatic and controlled retrieval processes in proactive interference

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ARTICLE INFO

Article history:
Accepted 18 March 2012
Available online 24 March 2012

Keywords:
Episodic retrieval
Interference
Control
Conceptual priming
Event-related potential
N400

ABSTRACT

Interference between competing memories is a major source of retrieval failure, yet, surprisingly little is known about how competitive memory activation arises in the brain. One possibility is that interference during episodic retrieval might be produced by relatively automatic conceptual priming mechanisms that are independent of strategic retrieval processes. Such priming-driven interference might occur when the competing memories have strong pre-existing associations to the retrieval cue. We used ERPs to measure the neural dynamics of retrieval competition, and investigated whether the ERP correlates of interference were affected by varying task demands for selective retrieval. Participants encoded cue words that were presented either two or four times, paired either with the same or different strongly associated words across repetitions. In a subsequent test, participants either selectively recalled each cue's most recent associate, or simply judged how many times a cue had been presented, without requiring selective recall. Interference effects on test performance were only seen in the recall task. In contrast, ERPs during test revealed an early posterior positivity for high interference items that was present in both retrieval tasks. This early ERP effect likely reflects a conceptual priming-related N400 reduction when many associations to a cue were pre-activated. A later parietal positivity resembling the ERP correlate of conscious recollection was found only in the recall task. The results suggest that early effects of proactive interference are relatively automatic and independent of intentional retrieval processes, consistent with suggestions that interference can arise through conceptual priming.

1. Introduction

Interference between competing memories has long been considered a major cause of memory failure in short-term and long-term memory. During retrieval of individual episodes or concepts from long-term memory, interference is thought to occur because a retrieval cue activates multiple associated memories that compete for conscious access. Such competitive activation reduces the probability that a particular target memory is successfully remembered (Anderson, 1983; McGeoch, 1942; Mensink and Raajimakers, 1988). Because competitive memory activation is unintentional and in direct conflict with the goals of the rememberer, it can be characterised as a relatively automatic process once

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doi:10.1016/j.brainres.2012.03.043

it is set in motion (Kahneman and Treisman, 1984; Posner and Snyder, 1975). In order to overcome interference, people are thought to engage strategic control mechanisms to select between competing memories (e.g. Anderson, 2003; Jonides and Nee, 2006). However, interference resolution attempts are often only partially successful since target memories often remain inaccessible despite efforts, suggesting that there are limitations to the intentional control over competitive memory activation. A large body of behavioural literature has demonstrated the major role that interference plays in memory, but relatively little is known about the underlying neural mechanisms of competitive activation and interference resolution. In the current study, we used the excellent temporal resolution of event-related potentials (ERPs) to investigate the real-time dynamics of automatic and strategic neurocognitive processes in retrieval interference.

Episodic memory interference is often studied with the classic AB AC paradigm, where participants are first trained on pairs of cue (A) and associate (B) stimuli such as words or pictures. Subsequently, participants are trained on A cues again, but this time paired with an alternative associate (C). Memory performance for these interference pairs is compared to performance for control pairs that are presented only once, and thus not subject to interference. In a subsequent recall test, presenting participants with the cue A and asking them to remember the first associate B gives an estimate of retroactive interference, that is, the interfering effect that learning new associations has on older memories. Testing the most recent associate C gives an estimate of proactive interference, that is, the interfering effect that older associations have on newer memories. Typically, participants show a large impairment of memory for B and C associates (depending on which item is being tested) compared to associates in the control condition and often erroneously recall non-target associates, which is thought to be caused by a failure to overcome competitive activation of both B and C at the time of retrieval (see Anderson and Neely, 1996; Crowder, 1976, for reviews).

There is now considerable evidence that multiple memory processes – ranging from intentional and typically conscious, to automatic and not necessarily conscious – support memory performance (Jacoby, 1991; Squire, 2004). Some early research indicated that interference is restricted to intentional recall ("in response to A, please remember associate C"), and does not occur on incidental tests of word associations (e.g. "in response to A, please report the first word that comes to mind"), at least when the competing associations had no pre-existing semantic relationships to the cue word (Graf and Schacter, 1987). Since incidental tests are thought to rely heavily on automatic memory processes such as priming (Tulving and Schacter, 1990), this finding has been interpreted as evidence that automatic memory is immune to interference (see discussion in Lustig and Hasher, 2001a). However, more recent research has shown that incidental tests are sensitive to interference in some circumstances (e.g. Lustig and Hasher, 2001b), suggesting that interference can be driven by automatic activation of competing memories in the absence of intentional retrieval attempts. Such rapid automatic activation of competing memories is behaviourally dissociable from the slower strategic control processes involved in resolving interference (Ikier, et al., 2008; Lustig, et al., 2004). Moreover, although incidental and intentional tests may tap automatic and controlled retrieval processes to different extents, multiple memory systems are likely to be coactive in any one test situation (Jacoby, 1991). These different memory systems appear to interact in complex ways, sometimes cooperating but other times competing in their influence on behaviour (Henson and Gagnepain, 2010; Poldrack and Packard, 2003). Winocur and others (e.g. Mayes et al., 1987; Winocur, et al., 1996) have suggested that interference during intentional episodic retrieval can nevertheless be driven by automatic conceptual priming of competing memories, if those competing memories have strong pre-existing associations to the retrieval cue.

Neuroimaging studies of retrieval interference have primarily focused on interference resolution mechanisms rather than competitive activation (although see Kuhl, et al., 2011). A large body of fMRI literature now indicates that lateral prefrontal regions are involved in strategic control of interference in both short-term and long-term memory tasks (e.g. Dolan and Fletcher, 1997; Henson, et al., 2002; Kuhl, et al., 2007; Wimber, et al., 2009; for reviews see Jonides and Nee, 2006; Badre and Wagner, 2007). However, because of the slow haemodynamic response, fMRI methods are unable to measure neural activation at the timescale necessary for distinguishing early automatic from later strategic retrieval processes. A few studies have investigated retrieval interference using EEG, which has excellent temporal resolution. Some of these studies focused on ERPs during associative encoding in the face of interference (Rössner et al., 2000; Uhl et al., 1990) and/or did not find significant correlates of interference at retrieval (Rössner et al., 2000; Tendolkar, et al., 1997). Others investigated ERP correlates of interference on a recognition test (Norman, et al., 2008) or the effect of "fan" size on slow-drift ERPs (Khader, et al., 2007). Using the retrieval-induced forgetting task, retrieval in the face of competition has been associated with prefrontal positive slow-drifts thought to index interference resolution (Johansson, et al., 2007), and fronto-central theta power increases that appear to index interference detection (Hanslmayr, et al., 2010; Staudigl, et al., 2010; see also Khader and Rösler, 2010).

In the current experiment, we focused on a different aspect of retrieval interference to those earlier studies by investigating whether ERP effects of proactive interference at retrieval would be manifest at a very early processing stage and independently of retrieval intentions, consistent with automatic priming driving competitive memory activation (Ikier et al., 2008; Lustig and Hasher, 2001a, 2001b; Lustig et al., 2004; Winocur et al., 1996). In order to elicit conceptual priming effects, we used cue-associate word pairs with strong pre-experimental relationships in a variant of the AB AC design while recording ERPs.

Prior ERP research has indicated that conceptual priming effects are typically expressed as a reduction of an ERP negativity between around 200–600 ms post-stimulus known as the N400 effect (Kutas and Hillyard, 1980). The magnitude of this N400 negativity is related to the degree of semantic memory system activation elicited by a meaningful stimulus (Kutas and Federmeier, 2011). Stimuli with many semantic associations produce larger N400 than stimuli with few semantic associations, suggesting that N400 size is correlated with the amount of conceptual information that is activated by a stimulus (Müller, et al., 2010). Pre-activation of associated conceptual information due to recent experience will reduce N400 negativity to a stimulus, with smaller N400s as the number of different pre-activated associations increases (Chwilla and Kolk, 2003; Kandhadai and Federmeier, 2008). These functional characteristics mean that the amount of N400 reduction for a stimulus relative to control can be used as a measure of the extent to which conceptual information associated to that stimulus is primed (Kutas and Federmeier, 2011). Priming-related N400 effects are seen in indirect tasks that do not require intentional retrieval, suggesting that they reflect a relatively automatic memory process (Guillem, et al., 2001). Furthermore, N400 priming-effects, though not the later left parietal ERP positivity thought to index episodic recollection, have been observed in patients with organic amnesia and impaired conscious recollection (Olichney, et al., 2000). Therefore, if interference in an episodic retrieval task can be driven by conceptual priming of pre-existing associations, we would expect reduced N400 negativities (i.e. more positive ERPs in the N400 time-window) to be associated with higher levels of behavioural interference.

We also aimed to assess whether ERP correlates of retrieval interference would be sensitive to task requirements to select one of the multiple competing memories associated to a cue. As previous research had indicated that interference through associative priming can occur independently of retrieval intention (Winocur et al., 1996), early ERP effects related to competitive activation might be elicited in response to cue words with multiple primed associations irrespective of whether the task requires associative recall. In contrast, strategic processes during retrieval, such as those related to intentional recall or interference resolution (e.g. Guillem, et al., 2001; Johansson, et al., 2007; Olichney et al., 2000), should only be engaged in situations where the task requires recall of a specific associate memory.

In order to address the above issues, participants encoded cue words that were presented either two or four times, either with the same or different associate words across repetitions. In the subsequent tests, participants were asked to either specifically recall each cue's most recent associate (i.e. a typical proactive interference AB AC intentional retrieval task, henceforth referred to as the “Recall” task) or to simply judge how many times a cue had been presented (a “judgement of frequency” [“JoF”] task, e.g. Hintzman and Curran, 1994; Hintzman, et al., 1982). It was reasoned that recalling the most recent associate should rely heavily on strategic memory processes such as intentional recollection attempts and interference resolution between competing memories. Cue frequency judgements on the other hand should require less strategic control since such judgements are thought to rely more on heuristic, item-strength assessments than recollection (Dobbins, et al., 2004; Hintzman and Curran, 1994; although see Brown, 1995), and furthermore, should not require interference resolution in order to select a specific associate. Importantly, because this design completely crossed the number of cue repetitions with associate repetition or change, it allowed a separation of neural effects related to cue repetition from those related to associative interference (cf. Henson, et al., 2002). That is, neural effects related to associative interference should not be dependent on cue repetition per se, but should be specifically enhanced when cues are repeated with multiple different associates. Furthermore, manipulating cue repetition independently of associate status also allowed us to directly compare selective retrieval with judgements of cue frequency.

We predicted that repeating a word pair intact should lead to facilitation on the specific recall test as a function of increased repetitions. In contrast, pairing a cue word with different associates should lead to impaired accuracy and elevated intrusion rates on the specific recall test as a function of increased repetition, due to proactive interference from the increasing number of associates to the same cue.[1] Such facilitatory or interfering effects on behaviour were expected to be less pronounced on the judgement of frequency task, if performance on this task primarily relied on assessing memory strength for the cue (Dobbins et al., 2004; Hintzman and Curran, 1994). For ERPs elicited by cue words during retrieval, effects related to conceptual priming were expected to be manifest as reduced N400 negativities (Kutas and Federmeier, 2011). If episodic interference can be driven by conceptual priming, such early relative ERP positivities should be particularly enhanced for items associated with the highest level of retrieval interference, i.e. cues presented four times with different associates. Moreover, because conceptual priming is considered a relatively automatic process, early interference-related ERP effects might be relatively insensitive to retrieval task. In contrast, ERP effects related to strategic retrieval processes were expected to be restricted to the recall task, and should be manifest primarily at a later processing stage than automatic priming effects.

2. Results

Behavioural and ERP data from retrieval test phases[2] were analysed with a 2×2×2 design with factors Cue Repetition (Two/Four; i.e. whether a cue word had been presented twice or four times during study), Associate Status (Same/Different; i.e. whether a cue word was presented with the same or

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[1] Note that the critical prediction for demonstrating proactive interference is a reduction in performance for cues presented with four different associates versus two different associates, and not the main effect of presenting the cue word with same or different associates. This is because such a main effect may be produced by facilitation effects for intact pairs presented multiple times. Furthermore, for repeated pairs, it is not possible to determine whether participants truly recalled the most recent presentation of the pair or a previous presentation of the same pair, since the latter would still be scored as correct. Thus, a main effect between same and different pairs cannot be unambiguously interpreted.

[2] We focused our analysis on behavioural data from the test phases since these data are most relevant to our hypotheses. Although we did collect subjective ratings of cue-associate pair strength during the study phase, these measures are not very informative since the cue repetition manipulation is likely to have biased participants' response criteria for such ratings (i.e., their rating criteria would likely have been affected by prior exposure to the same cue or cue-associate pair). For the record however, there were no significant differences in ratings that could explain our behavioural or ERP results at test.

different associates during study repetitions) and Retrieval Task (JoF/Recall; i.e. whether participants were instructed to judge the number of times a cue had been presented or recall its most recent associate).

2.1. *Behavioural results*

Post-experiment questionnaire data showed that participants did not judge there to be any difference in difficulty or success between the JoF and Recall tasks (both ts < 1). Participants reported that seeing a cue with the same or different associates had a numerically larger effect on their performance on the Recall task than the JoF task, but this did not reach significance (t(23) = 1.6, P = 0.13).

Retrieval test accuracy is presented in Fig. 1, where it can be seen that, consistent with the self-reports, the Same/Different associate and Cue Repetition manipulations primarily affected performance in the Recall task.

A three-way ANOVA with factors Associate Status (Same/Different), Retrieval Task (JoF/Recall) and Cue Repetition (Two/Four) revealed a highly significant three-way interaction in the accuracy data (F(1,23) = 18.9, P <0.0001). To clarify this interaction, two-way Cue Repetition × Associate Status ANOVAs were calculated separately for the two retrieval tasks. There were no significant main effects or interactions on the JoF task (all Fs < 1), but highly significant main effects on the Recall task of Repetition (F(1,23) = 13.1, P <0.001), Associate Status (F(1,23) = 54.9, P <0.0001), and a highly significant Repetition × Associate Status interaction (F(1,23) = 56.0, P < 0.0001). Follow-up simple comparisons revealed that for cues presented with the Same associate, there was a trend for facilitation as a function of repetition, whereby Four repetitions led to higher Recall accuracy than Two repetitions, albeit this difference just failed to reach significance (t(23) = 2.0, P = 0.06). For cues presented with Different associates, Recall accuracy for cues that had been presented Four times was significantly lower than for cues that had been presented Twice (t(23) = 6.3, P < 0.0001).

The majority of Recall errors committed in both Different conditions were intrusions (i.e. erroneously reporting of other associates than the most recent), with significantly more intrusion errors for Four repetition than Two repetition cues (proportion intrusions 0.36 [SEM = 0.04] and 0.16 [SEM = 0.04] respectively, t(23) = 7.4, P < 0.0001). Recall intrusion rates in the Same conditions were very low (<0.02) and not significantly different (t < 1), as expected.

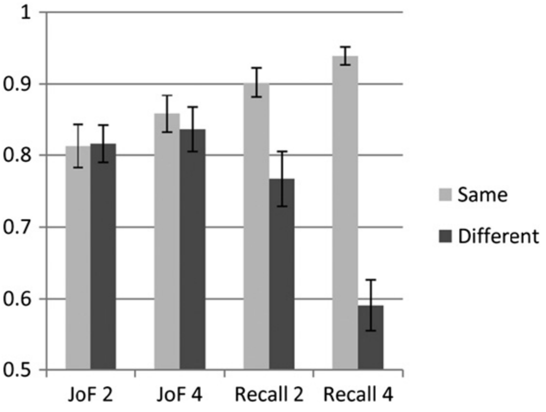

Fig. 1 – Proportion accurate responses across the Judgement of Frequency and Recall tasks dependent on Cue Repetition and Associate Status. Error bars depict the standard error of the mean.

In sum, the retrieval test results showed that there were no effects of number of cue repetitions and whether or not that cue was presented with the same or different associate across repetitions on judgements of frequency, but there was a predicted pattern of effects on the intentional recall task. Increasing the number of repetitions of a cue with the same associate improved recall, albeit not quite significantly so. In contrast, increasing the number of different associates to a cue decreased recall accuracy and increased intrusion errors, consistent with interference from competing activation impairing performance.

2.2. *ERP results*

Grand average ERPs for the Recall (Fig. 2) and JoF tasks (Fig. 3) showed that in both tasks, the condition associated with the highest behavioural interference (i.e. cues repeated four times with different associates) had the most positive ERPs between ~200 and 600 ms post-stimulus.

Topographic difference maps (Fig. 4) showed that this early ERP difference between Same and Different associate conditions appeared to be specific to cues that had been repeated four times (dashed boxes) with no similar effect for cues presented twice. The early positivity was of larger magnitude with a broader, more anterior distribution in the Recall task than in the JoF task.

Cue Repetition seemed to enhance prefrontal positivity in the early time-window irrespective of Associate Status, in particular in the Recall task (Fig. 2). Furthermore, cues presented with the same associate or with four different associates elicited enhanced late positive slow-drifts in the Recall task only, with no similar slow-drift effects in the JoF task (cf. Figs. 2 and 3).

2.3. *Partial least squares statistical results*

Non-rotated Partial Least Squares (PLS) multivariate statistical analyses (McIntosh and Lobaugh, 2004) were conducted on the global spatiotemporal ERP data separately for early (0–600 ms) middle (600–1200 ms) and late (1200–1800 ms) time-windows using the full factorial design. The results of these analyses (Table 1) confirmed that in the early 0–600 ms time-window, in addition to significant main effects of Cue Repetition and Associate Status, there was also a significant interaction between Cue Repetition and Associate Status, which did not interact with Retrieval Task.

Fig. 5 shows the reliability of the significant main effects and interaction in the early window across the spatiotemporal data, as indexed by the ratio of the PLS electrode saliences against their bootstrapped standard error.

This bootstrap test showed that the main effect of Cue Repetition (Fig. 5A) was reliable across the prefrontal scalp from approximately 150 ms after stimulus presentation, with more positive ERPs for cues repeated four than two times.

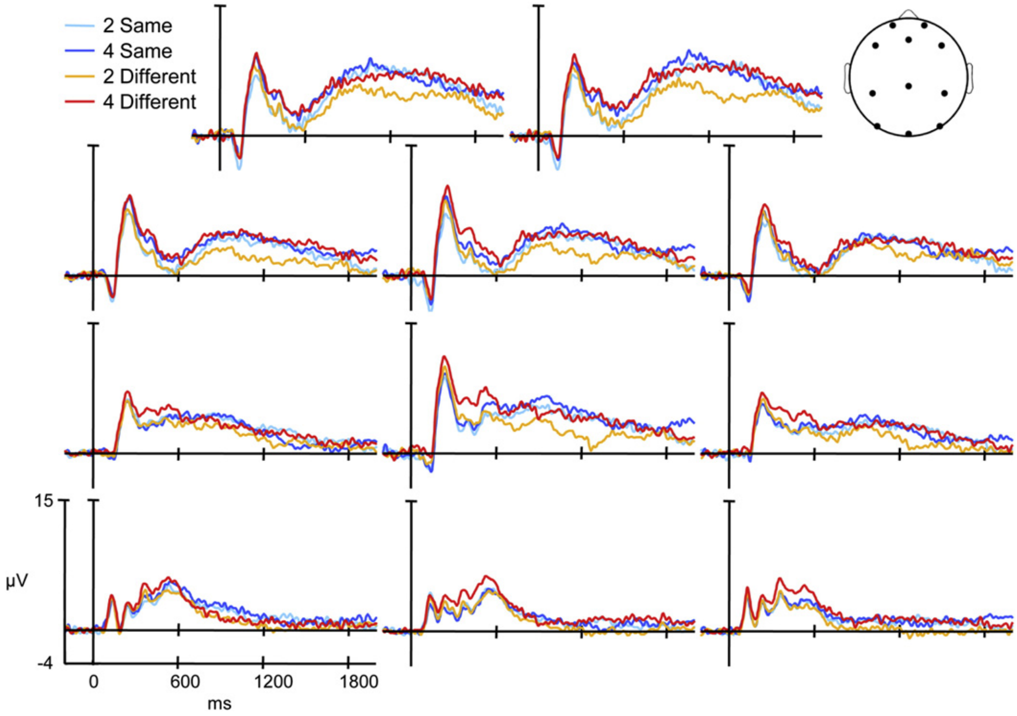

Fig. 2 – Grand average ERPs in the Recall task, separated by Cue Repetition and Associate Status.

The effect of Associate Status (Fig. 5B) emerged across occipital sites around the same time, and later took a more centroparietal distribution, maximal between 200 and 500 ms post-stimulus. The interaction between Cue Repetition and Associate Status was maximally reliable across the occipital, parietal and central scalp between 300 and 600 ms (Fig. 5C), confirming that the effect of Same/Different associate on early posterior ERPs was reliably different across cues repeated two or four times.

To verify that this early ERP interaction was indeed driven by the increased centroparietal positivity specifically for high interference items, and that the effect was significant in

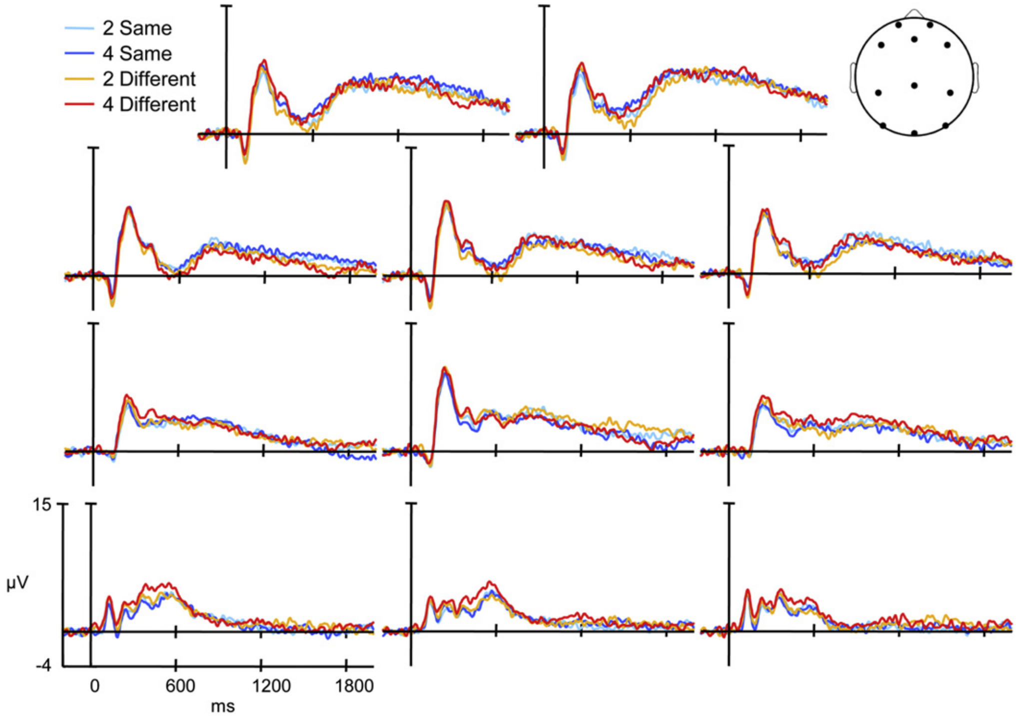

Fig. 3 – Grand average ERPs in the judgement of frequency task, separated by Cue Repetition and Associate Status.

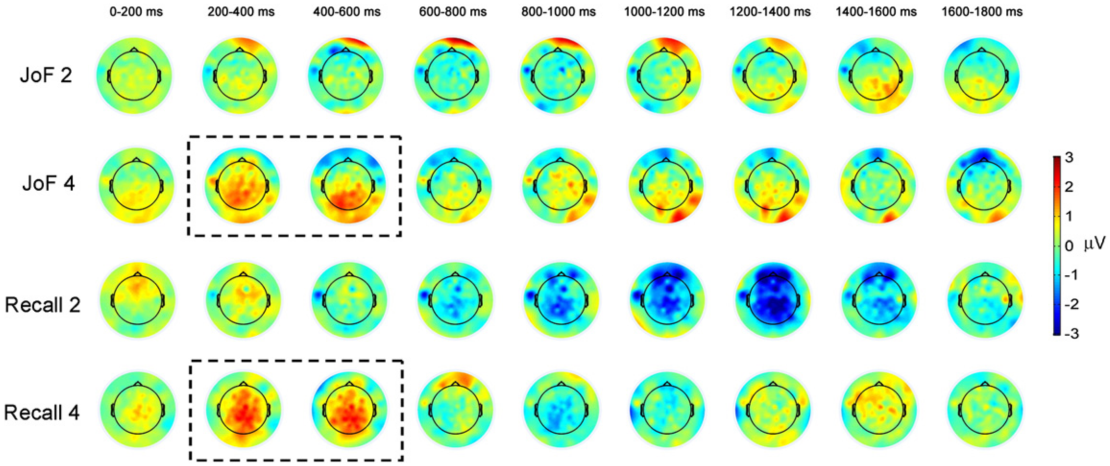

Fig. 4 – Topographic maps plotting the scalp distributions of the ERP amplitude difference between cues presented with the same associate subtracted from cues presented with different associates. The dashed boxes show the early positivity for cues presented four times with different associates, which was elicited in both tasks.

both tasks, a second PLS analysed a targeted contrast comparing the high interference (Four Different) condition against the average of the other three lower interference conditions, separately for each task (Fig. 6). This targeted contrast was significant in both tasks, although the effect was stronger in the Recall (permuted $P<0.001$) than the JoF task ($P<0.05$).

In contrast to the early ERP effects of Cue Repetition and Associate Status, the Retrieval Task manipulation did not modulate ERPs significantly until the later 600–1200 ms and 1200–1800 ms time-windows (Table 1).[3] The bootstrap ratios for these significant effects (Fig. 7) showed that the Recall task was associated with a sustained ERP positivity that had a left parietal maximum between ~600-900 ms, which later developed into a more diffuse distribution with a prefrontal contribution. Although this effect appeared to be driven by the Two Same, Four Same and Four Different conditions that had more positive late ERPs (Fig. 2) compared to the Two Different condition in the Recall task, the effect of Retrieval Task did not significantly interact with Associate Status.

In sum, the main ERP results revealed an early posterior positivity for high interference items that was elicited independently of retrieval task, an early frontal positivity associated with cue repetition, and a later sustained ERP positivity that was elicited in the Recall task only.

3. Discussion

We investigated the ERP correlates of automatic and strategic memory processes during retrieval in the face of interference from recently studied but pre-experimentally established associations. ERPs were recorded during a memory test while participants either selectively recalled a specific associated memory to a cue, or made a judgement of frequency on the cue itself. Retrieval competition produced a large impairment to specific recall but had no effect on cue frequency judgements, consistent with the suggestion that frequency judgements primarily involve an assessment of cue strength (Dobbins et al., 2004; Hintzman and Curran, 1994), and thus would be relatively insensitive to processes affecting associative recall. Despite the different pattern of behavioural interference across the tasks, an early ERP positivity was elicited by cues with multiple previously studied associations in both tasks. This latter finding suggests that associated memories were activated to some extent in response to test cues even when associative recall was irrelevant for task performance, consistent with the notion that retrieval interference involves automatic priming mechanisms that are separable from intentional retrieval processes (Ikier, et al., 2008; Lustig and Hasher, 2001a, 2001b; Lustig, et al., 2004; Winocur et al., 1996).

The early ERP positivity for high interference items resembles the N400 reductions typically observed in conceptual priming tasks, where a meaningful stimulus elicits a smaller N400 as a consequence of prior exposure to related information (Kutas and Federmeier, 2011). Such N400 reductions are thought to index facilitated activation of associated information due to conceptual priming. In the context of the current experimental design, reduced N400s to high interference items indicate that presenting multiple associates to a cue during study facilitated activation of those associations at test, with N400 size decreasing as the number of primed associations increased. This pattern is consistent with previous research that has shown that multiple related primes reduces N400 effects to a target more than a single related prime (Chwilla and Kolk, 2003; Kandhadai and Federmeier, 2008), and is compatible with the view that N400 size reflects the sum of stimulus-elicited conceptual activation (Kutas and Federmeier, 2011).

Similar early posterior ERP positivities (or “reduced negativities”) in episodic retrieval tasks have previously been ascribed to implicit, automatic memory processes since they can be elicited in the absence of retrieval facilitation and

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[3] However, there was a near significant trend (see Table 1) for an interaction between Cue Repetition and Retrieval Task in the early time window, which seemed to be produced by a larger effect of Cue Repetition in the Recall than the JoF task across prefrontal electrodes, cf. Figs. 2 and 3.

Table 1 – PLS results across early, middle and late time-windows. The table shows the percent of covariance accounted for by each PLS contrast and its associated significance value as estimated by 1000 permutations. Statistically significant effects are highlighted in bold.

Contrast	0–600 ms		600–1200 ms		1200–1800 ms	
	Covar. (%)	P-value	Covar. (%)	P-value	Covar. (%)	P-value
Cue repetition	**21.67**	**0.020**	19.07	0.062	12.39	0.214
Retrieval task	9.80	0.262	**19.27**	**0.036**	**25.95**	**0.018**
Associate status	**26.01**	**0.003**	14.28	0.134	8.97	0.444
Repetition*task	13.89	0.078	15.61	0.114	12.35	0.232
Repetition*associate	**16.87**	**0.035**	11.22	0.318	14.52	0.136
Task*associate	7.02	0.644	14.13	0.165	12.41	0.218
Repetition*Task*associate	4.74	0.988	6.42	0.859	13.42	0.169

conscious awareness of prior experience (Rugg et al., 1998; Stenberg, et al., 2000; Woollams, et al., 2008; Yu and Rugg, 2010). When these ERP positivities have a relationship to behaviour however, they typically correlate with improved explicit memory performance (see Paller, et al., 2009, for discussion). In our study, early positivities were elicited in the absence of performance differences on a frequency judgement task, but were associated with *impaired* performance on a specific recall task. The recall results may thus be an example of conflict between automatic and controlled memory processes (Jacoby, 1991; Poldrack and Packard, 2003). It appears that due to their exposure in the study phase, multiple pre-existing associations to a cue were primed at test. Such priming had no measurable effect on frequency judgements, perhaps because when focusing on making a heuristic judgement of cue strength, primed associations were not consciously retrieved, or perhaps because participants judged associative information to be non-diagnostic of cue repetition. However, when attempting to recall a specific associate, conceptual priming of multiple associations impeded the episodic system's ability to select the specific target episode, leading to impaired recall performance. These differences across tests and experiments illustrate how episodic and semantic memory systems may interact differently in guiding behaviour depending on the goals of the rememberer (Henson and Gagnepain, 2010). The current findings are to our knowledge the first ERP evidence in support of the notion that conflict between conceptual priming and episodic memory may impair memory performance.

Our findings are consistent with previous suggestions that conceptual-priming driven interference is mediated by a cortical memory brain network that is separable from the medial temporal episodic memory network (Winocur et al., 1996). Evidence for this view includes the finding that severely amnesic patients with medial temporal lobe damage show intact and sometimes even increased retrieval interference compared to controls when the competing memories involve pre-existing associations (Kinsbourne and Winocur, 1980; Mayes, et al., 1987; Warrington and Weiskrantz, 1974; Winocur and Weiskrantz, 1976; Winocur et al., 1996). In fact, one major function of the episodic network may be to counteract cortical interference through the establishment of distinct, separable

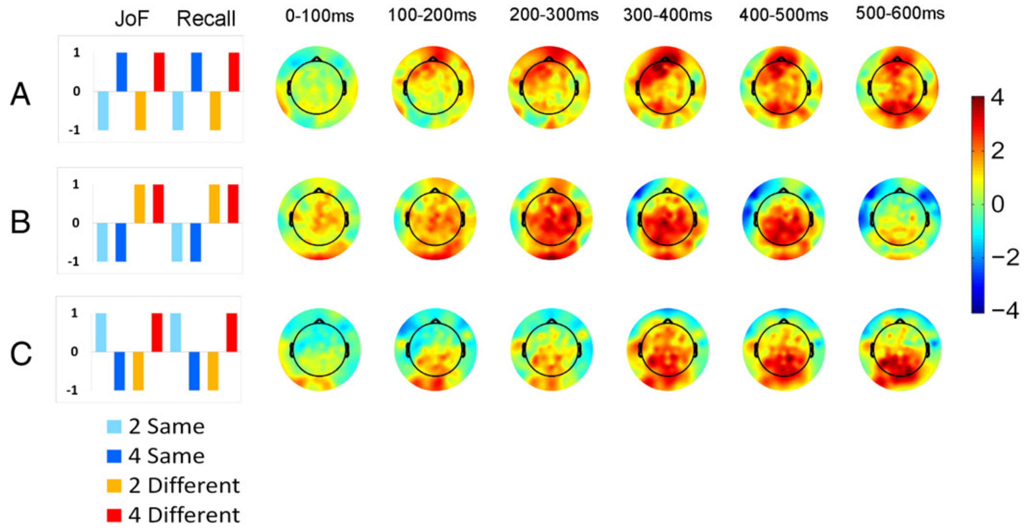

Fig. 5 – Significant PLS contrasts in the 0–600 ms time-window, and their electrode salience to bootstrapped standard error ratios. A, the main effect of Cue Repetition; B, the main effect of Associate Status and C, the Cue Repetition*Associate Status interaction. The bootstrap ratios are approximately equivalent to z-scores, values > 1.96 indicate electrodes that reliably show the pattern expressed in the associated contrast, with more positive ERPs for conditions with a positive contrast score, and vice versa. Values < −1.96 indicate electrodes that reliably show the reverse pattern to the associated contrast, with more negative ERPs for conditions with a positive contrast score, and vice versa.

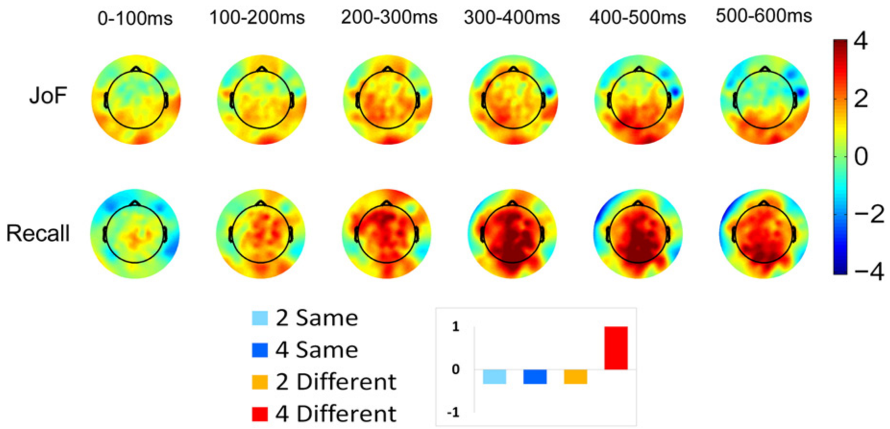

Fig. 6 – The targeted PLS contrast comparing the high interference against the other three conditions in the early time-window was significant in both tasks. The scalp maps of the associated electrode salience to bootstrapped standard error ratios show that the posterior positivity was rather subtle but reliable in the JoF (top) task, and highly reliable in the Recall (bottom) task.

memory traces (McClelland, McNaughton and O'Reilly, 1995). At retrieval, recollection of distinct episodic traces may be used strategically to overcome priming-driven interference (öztekin, Curtis, and McElree, 2008), explaining the aforementioned increased susceptibility to interference seen after hippocampal damage (e.g. Winocur et al., 1996).

In contrast to the early posterior ERP effects of associative interference, cue repetition reliably enhanced prefrontal ERPs from approximately 150 ms after presentation, suggesting that cue repetition, and whether or not that cue was presented with the same associate across repetitions, produced separable neural effects at subsequent retrieval. This early repetition effect showed a trend towards being larger during recall than frequency judgements, although the interaction with task was not strictly significant. Frontal positivities in response to item repetition have been related to context-free episodic memory for item familiarity (Curran, 2000; Smith and Guster, 1993; see Rugg and Curran, 2007 for review; although see Voss and Federmeier, 2011), which would be consistent with our finding that this frontal repetition effect appeared to be independent of associative interference. However, familiarity-related ERP effects tend to emerge somewhat later than the current effect (they typically have a 300–500 ms post-stimulus maximum, Rugg and Curran, 2007). Also, there is no obvious reason why familiarity-related processes should trend towards being enhanced in the recall task. Instead, the effects resemble very early repetition-related frontal ERP positivities that have been described previously as separate from familiarity-related effects (e.g. Tsivilis, et al., 2001), and are enhanced during intentional retrieval (Guillem et al., 2001). These ERP effects have been suggested to reflect a retrieval search attempt that is elicited only if a cue is deemed sufficiently familiar to warrant a memory search based on a very rapid "feeling-of-knowing" signal (Diana, et al., 2005; Paynter, et al., 2009).

Significant ERP modulations dependent on retrieval task emerged only late in the epoch, but these effects were not uniquely associated with high levels of interference, so are unlikely to reflect intentional interference resolution (c.f. Johansson et al., 2007). Instead, the Recall task seemed to be generally associated with a late positive slow-drift with an initial left parietal topography that turned into a broader diffuse pattern with a frontal contribution. Left parietal positivities are typically associated with episodic recollection in memory retrieval tasks (Rugg and Curran, 2007), and recollection-related effects often have rather diffuse sustained topographies in cued recall tasks (Allan and Rugg, 1997). If these late ERP positivities in the Recall task are related to recollection, this result indicates that the Recall task relied more on recollection than the JoF task, consistent with the behavioural dissociation between the two tasks and with previous suggestions that judgements of item frequency are often based on estimates of item strength (i.e. familiarity) rather than recollection (Dobbins, et al., 2004; Hintzman and Curran, 1994; although see Brown, 1995). The results also converge with previous reports that the relatively automatic associative process indexed by N400 reductions occurs in both

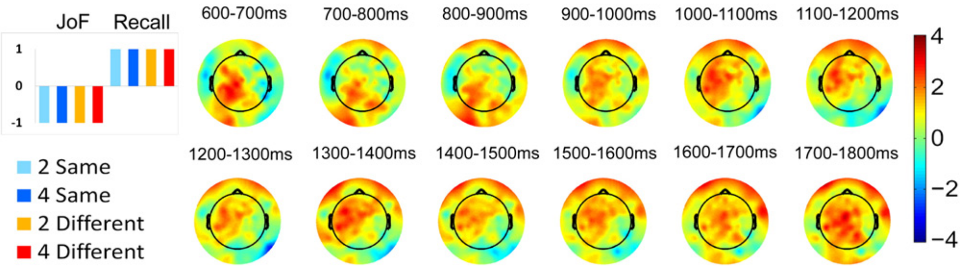

Fig. 7 – The retrieval task PLS contrast that was significant in the two late time-windows, and its associated electrode salience to bootstrapped standard error ratios.

incidental and intentional retrieval tests, whereas the later recollection-related parietal positivity is enhanced by intentional retrieval (Guillem, et al., 2001). However, this interpretation is necessarily tentative since there were also other differences between the two retrieval tasks. Nevertheless, regardless of the precise functional interpretation of the late slow-drift effect, the finding is consistent with the general hypothesis that strategic processes involved in performing the different memory tasks would be engaged primarily at a later retrieval stage than automatic competitive activation.

Although conceptual priming appears to best account for the interference-related early posterior ERP positivity, there are alternative explanations. Because the effect had a very early onset and was elicited in a task that did not require selective retrieval, it seems unlikely that it reflects intentional recollection of associated information or the strategic implementation of interference resolution. It might however index a precursor to interference resolution, such as the detection of high conflict items. Neuroimaging evidence suggests that interference involves separable conflict detection brain mechanisms that signal the need for control and conflict resolution brain mechanisms that execute control (Botvinick, et al., 2001). The early ERP effect might relate to the former. Because the retrieval tasks were randomly intermixed, participants may have failed to disengage this conflict detection mechanism on frequency judgement trials, even though the level of associative interference was irrelevant to this task. However, a large body of literature indicates that conflict detection is typically associated with early enhanced ERP *negativities* for high conflict items (e.g. Hanslmayr, et al., 2008; West, 2003; see Carter and Van Veen, 2007, for review), so we would expect conflict detection in the current task to modulate ERPs in the opposite polarity to the observed pattern.

One caveat in the current design that should be acknowledged is the difference in repetition spacing during study between the two repetition and four repetition conditions. Cues repeated four times were presented at shorter repetition lags than cues presented twice, which may have affected cued recall performance. When cue and associate pairs are unchanged across repetitions, increased repetition lag typically leads to enhanced cued recall (e.g. Raaijmakers, 2003), meaning that the longer repetition lag for two repetition pairs may have counteracted the beneficial effects of repetition on cued recall for four repetition pairs. For different associate pairs, the shorter lag for cues repeated four times might actually increase proactive interference, since cues that are encoded in temporally similar contexts may elicit more associated interference at retrieval than those encoded in temporally separate contexts (e.g. Lorsbach, 1990). Therefore, if spacing effects contribute to our results, we would expect such effects to increase retrieval interference for cues repeated four times with different associates compared to twice with different associates, consistent with our claim that the former items suffered the most retrieval interference. Such temporal context effects may however be considered a relatively episodic form of interference, and thus, future studies on conceptual priming contributions to retrieval interference should equate repetition lag between conditions.

One remaining open question is whether interference through conceptual priming leads to failures to consciously recall a target response (in line with the cue overload principle, Watkins and Watkins, 1975), or whether competing associations come to mind but participants are unable to correctly discriminate between them. Future research would need to assess recall of all associates to a cue in order to address this point. In theory, conceptual priming could impair conscious memory even when the intentional retrieval goal is to recall all associates to a cue. This is because conscious recall is a selective process, in that only one response can be at the focus of awareness at any moment. In order to report responses B and C when given cue A, these responses have to be selectively accessed in memory one at a time. Thus, when trying to consciously recall any one association, if multiple associations are automatically primed this will result in conflict between automatic and intentional retrieval processes.

Another question of interest is whether the early interference-related positivity is dependent on episodic retrieval mode (Tulving, 1983). Although we contrasted two tasks that differed in whether they required specific associative recall, both tasks did direct participants towards their prior experience of the cue word. Even though associative interference in the current paradigm seems to be driven by a relatively automatic process, it is possible that this process requires intentional episodic orienting in order to be set in motion (Cohen, et al., 1990; Kahneman and Treisman, 1984; Kiefer, 2008). Alternatively, if the early positivity is truly independent of episodic retrieval intention – as would be predicted if it is a pure index of conceptual priming in a semantic cortical network – it should also be elicited if cues with multiple primed associates were presented in a task without any intentional episodic retrieval requirements, as long as the cues were processed at a semantic level. Future research is also required to compare ERP correlates of retrieval interference across materials involving novel versus pre-existing associations. If the early ERP positivity indexes a type of associative priming that is critically dependent on pre-established conceptual associations, it should not be elicited in an interference situation where the materials are purely episodically related (e.g. Graf and Schacter, 1987).

In conclusion, the current experiment demonstrated that early neural effects that may reflect competitive memory activation through conceptual priming can be distinguished from later neural effects related to strategic retrieval processes in a proactive interference task. When such early automatic and late intentional retrieval processes are in conflict (Jacoby, 1991; Poldrack and Packard, 2003) this is manifest as episodic memory impairments. In contrast, when early automatic processes are irrelevant for intentional retrieval goals, they can be decoupled from behavioural performance. This pattern suggests that the degree to which different memory systems interact when influencing behaviour is goal dependent.

4. Experimental procedures

4.1. *Participants*

Twenty-four right-handed, healthy native English speakers (7 males, mean age 24 [range 18–35]) with normal or corrected-to-normal vision contributed to the final dataset. Three additional participants were replaced due to excessively noisy EEG data. Participants gave informed consent, and the investigation was approved by the University of Cambridge Psychology Research Ethics Committee.

4.2. *Stimuli*

Stimuli consisted of 160 cue words (e.g. "glow) and each cue's four most frequent associates (e.g. "worm, lamp, shine, warm") as generated by the computerised Edinburgh Associative Thesaurus (http://www.eat.rl.ac.uk). Associates were edited to ensure there were no duplicate stimuli, with the next most frequently reported associate taking the place of those removed. Assignment of stimuli to experimental conditions was fully counterbalanced across subjects.

4.3. *Procedure*

Participants were seated in a sound and light attenuated room, and completed a study-test practice cycle. Next, the EEG set-up was prepared, after which participants completed 10 study-test cycles of the experimental memory task with short breaks in between each block.

During each study phase, participants rated the strength of association between each cue and associate word pair on a four-point scale using a response button for either their left or right hand (counterbalanced across participants). This encoding task was chosen to enhance associative encoding. Sixteen cue words were presented in each block, four in each condition (twice with the same associate each time, four times with the same associate each time [Same conditions], twice with a different associate each time, or four times with a different associate each time [Different conditions]), semi-randomly intermixed in four cycles. Cue words with four repetitions were presented in all four cycles, whereas half of the cue words with two repetitions were presented in cycles one and three, and the other half in cycles two and four. Each study trial began with a 0.5 s fixation cross, after which the cue and associate word were presented centrally (cue above the associate) on the computer screen for 3 s. Participants were required to respond while the words were on the screen. Following each study phase, participants completed a 30 s counting distractor task.

During each test phase, participants were cued on a trial-by-trial basis (order randomized) to either estimate how many times they had encountered a particular cue word during the preceding study phase (Judgement of Frequency ["JoF"] task), or to try to remember the most recent associate that cue had been presented with during the study (Recall task). Each trial began with a fixation cross with a duration between 1 and 1.5 s,[4] jittered in 50 ms steps. Next, a prompt symbol (either an "O" or "X" shape) was presented for 2 s, indicating which retrieval task to complete on the trial (assignment of symbol to retrieval task counterbalanced across participants). The cue word was then displayed for 3 s, and followed by a "???" screen for 2 s, which signalled that participants should speak their answer out loud (in both tasks). Participants were asked to withhold their answer and only speak when the question mark screen appeared in order to avoid movement related artefacts in the critical ERP time-window. They were asked to say 'pass' if they could not remember the answer.

Following the experiment, participants completed three questionnaire items for each retrieval task. They rated how difficult they had found each task, how successful they thought they were at each task, and whether they thought that the same/different status of the associate words had an effect on their performance on each task (all on a 5-point scale).

4.4. *EEG recording and preprocessing*

EEG was recorded referenced to Cz using a Electrical Geodesic Netamps 200 system with a 128-channel HydroCel Geodesic Sensor Net. Signals were amplified with a bandwidth of 0.01–70 Hz (250 Hz sampling rate). Acquired data were analysed using EEGLAB 7 (Delorme and Makeig, 2004). The continuous EEG data from all blocks were concatenated, re-referenced to an average mastoid reference, filtered digitally with a band-pass of 0.3–30 Hz (two-way least-squares finite impulse response filter), and corrected for artefacts using extended infomax Independent Component Analysis (ICA; see Bergström et al., 2009b for details). Any trials that still contained visible artefacts following the artefact correction were removed. Only a very small proportion of trials (between 5 and 10%) were deleted in total after artefact rejection. Next, ERPs were formed separately for each experimental condition, time-locked to the onset of the cue word[5] and baseline corrected for the 200 ms pre-stimulus interval. These ERPs included all artefact free trials irrespective of accuracy. At a practical level, averaging across both accurate and inaccurate trials allowed us to retain an adequate number of trials per ERP average and to equate signal-to-noise ratios across all conditions. At a theoretical level, it was reasoned that interference-related effects such as competitive activation and interference resolution should be even more pronounced on inaccurate than accurate trials, so including only accurate trials would dilute interference-related ERP effects[6] (see Henson et al., 2002, for a similar argument). Mean trial numbers were between 18 and 19 for all conditions and no participant had fewer than 13 trials contributing to any condition.

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[4] The fixation cross was jittered in order to increase the signal-to-noise ratio of ERP effects of interest by preventing time-locking of EEG alpha activity unrelated to the manipulation.

[5] We were also interested in whether the prior prompt to either recall an associate or make a judgement of frequency would elicit ERP correlates of preparatory processes that might differ depending on retrieval orientation (e.g. Herron and Wilding, 2004). We therefore also analysed ERPs time-locked to the prompt symbols. However, there was no indication of differences in prompt-elicited ERPs, thus these data are not presented. This null result actually makes the cue word-locked ERPs presented here easier to interpret in that the latter effects cannot be caused by differences in pre-retrieval ERP amplitudes.

[6] A follow-up analysis (not presented) included only accurate trials in order to verify that the main results were not simply produced by differences in accuracy between conditions. When keeping accuracy constant, the ERPs showed a very similar pattern to that presented here, although with only trend-level reliable effects due to the decreased signal-to-noise ratio caused by lower trial numbers per condition.

4.5. *ERP statistical analysis*

The main ERP statistical analysis was conducted using 'non-rotated' spatiotemporal Task Partial Least Squares (PLS), a multivariate statistical technique that allows examination of distributed patterns of spatial and temporal dependencies in the ERP data (Bergström et al., 2007, 2009a, 2009b; Lobaugh, et al., 2001; McIntosh and Lobaugh, 2004; McIntosh et al., 1996). PLS analyses the "cross-block" covariance between a matrix of dependent measures (the spatiotemporal ERP distribution) and a set of exogenous measures, in this case orthogonal contrast vectors representing the experimental conditions (the number of contrasts equal to the degrees of freedom in the experimental design), thereby constraining the solution to covariance attributable to the experimental manipulation (McIntosh and Lobaugh, 2004). In nonrotated PLS (Bergström et al., 2009a, 2009b; McIntosh and Lobaugh, 2004) the sums of squares of the cross-block covariance between the contrast vector and the spatiotemporal data matrix are directly tested for significance using random permutation test, thus allowing a direct assessment of the hypothesised experimental effects. The PLS analysis outputs electrode saliences which identify the electrodes that most strongly covary at a particular point in time with the experimental effect expressed in the contrast vector. The standard errors of the electrode saliences are estimated through bootstrap resampling. The ratio of the electrode salience to the bootstrap standard error gives a standardized measure of reliability that is approximately equivalent to a z score, whereby values above 1.96 and below −1.96 are reliably different from zero with a 95% confidence interval (McIntosh and Lobaugh, 2004).

In the current analysis, non-rotated PLS was first used to test the full factorial design, with contrasts coding for main effects of Retrieval Task (JoF/Recall), Associate Status (Same/Different) and Cue Repetition (Two/Four) and their 2-way and 3-way interactions (7 contrasts in total). EEG data were separated into early (0–600 ms), middle (600–1200 ms) and late (1200–1800 ms) time-windows for increased temporal resolution, and the covariance of the experimental contrasts with the spatiotemporal data in each time window was tested for significance using 1000 permutations. The full factorial analysis was followed up with a targeted PLS analyses directly testing the main hypothesis. The reliability of the electrode saliences was tested using 200 bootstraps. See McIntosh and Lobaugh (2004) for full description of PLS. Matlab code to perform PLS is available at http://www.rotman-baycrest.on.ca/pls.

Acknowledgments

We thank Michael C. Anderson, Richard N. Henson, Jason R. Taylor and Maria Wimber for helpful comments on data interpretation and the manuscript, and Joe Farrington and Anna Tweed for developing stimuli and piloting the task. This work was supported by the BBSRC [grant number BB/G014795/1], and was carried out in the Behavioural and Clinical Neuroscience Institute, supported by a joint award from the MRC and the Wellcome Trust.

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