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Research Report

ERP correlates of recognition memory: Effects of retention interval and false alarms

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ABSTRACT

Within the framework of the dual process model of recognition memory, prior work with event-related potentials (ERPs) has suggested that an early component, the FN400, is a correlate of familiarity while a later component, the Late Positive Complex (LPC), is a correlate of recollection. However, other work has questioned the validity of these correlations, suggesting that the FN400 effect is too short-lived to reflect an explicit memory phenomenon and that the LPC may be influenced by decision-related factors. Using a Remember/Know paradigm we addressed these issues by (1) examining the effect of study-test delay on correctly recognized items associated with familiarity ('Know' responses) and recollection ('Remember' responses) and by (2) examining FN400 and LPC modulation associated with false alarms. Supporting the relationship of the FN400 with familiarity, attenuation of this component was present for 'Know' responses relative to correct rejections after both the short (39 min) and long (24 h) delay conditions. Attenuation of the FN400 also occurred for false alarms (responses largely driven by familiarity) relative to correct rejections. Although an increased LPC amplitude was found associated with 'Remember' responses at both delays, a decreased LPC amplitude was observed with false alarms relative to correct rejections. This latter result is discussed with regard to the possibility of an overlapping posterior negativity.

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1. Introduction

Dual process models of recognition memory posit that recollection and familiarity are separate processes (Jacoby, 1991; Mandler, 1980; Yonelinas, 2002). Familiarity is frequently described as a sense of prior exposure lacking contextual details while recollection is thought to support detailed retrieval of a study episode. Such dual process accounts were created to explain data inconsistent with more parsimonious single process descriptions of episodic memory. Although dual process models remain controversial, they are supported by data from a variety of sources, including rodent and primate studies (Brown and Aggleton, 2001; Fortin et al., 2004), lesion studies in patients with amnesia (Holdstock et al., 2002; Yonelinas et al., 2002), functional magnetic resonance imaging [fMRI; (Cansino et al., 2002; Davachi et al., 2003; Ranganath et al., 2004; Wheeler and Buckner, 2004)], and event-related potentials [ERPs; (Curran, 2000; Duarte et al., 2004; Duzel et al., 1997; Rugg et al., 1998a)].

ERP studies have provided, perhaps, some of the most convincing evidence that recollection and familiarity are separate processes. In general, ERPs are more positive 300 ms after presentation of correctly recognized studied items compared to correctly rejected non-studied items (Rugg, 1995). This difference has been termed the 'ERP old/new effect'. Several groups have found spatially and temporally distinct ERP modulations within the old/new effect that appear to be specifically associated with familiarity and recollection, respectively. An early (~300–500 ms) component is correlated with familiarity while a later (~500–800 ms) component appears modulated by recollection (Curran, 2000, 2004; Curran et al., 2001; Duzel et al., 1997; Rugg et al., 1998a; Wilding and Rugg, 1997a).

The familiarity correlate is similar in latency and polarity to the N400 described in studies of language processing and semantic priming (Holcomb, 1993; Kutas and Hillyard, 1980; Rugg and Doyle, 1994), and tends to be more anteriorly distributed in some, but not all studies (Curran and Cleary, 2003; Duzel et al., 1997; Finnigan et al., 2002; Nessler et al., 2001; Rugg et al., 1998a). The reason for differences in topography is unclear, but may in part be related to differences in stimuli, how familiarity was operationalized in these studies, and the referencing technique used; the latter a general issue for comparing topographies across ERP studies [for example, average referenced ERPs versus ERPs referenced to mastoid electrodes; see (Curran, 1999; Finnigan et al., 2002)]. Because of its similarity with the N400, some have designated this correlate the FN400 (for the sake of clarity, we will use this designation throughout the manuscript). Responses associated with familiarity reduce, or attenuate, the negative amplitude of this component.

Support for the relationship of the FN400 with familiarity has come from studies using a variety of different experimental methodologies. For example, several studies have demonstrated comparable FN400 attenuation for both studied items and non-studied, similar 'lures' relative to non-studied, unrelated items (Curran, 2000; Curran and Cleary, 2003; Curran et al., 2002; Nessler et al., 2001). Similar lures are assumed more familiar than unrelated items, as exemplified by the higher rate of incorrect 'Old' endorsements (false alarms) to these items.

Other studies have utilized the 'Remember/Know' paradigm (Gardiner, 1988; Tulving, 1985) in which subjects report introspectively the basis of their recognition judgments. Participants are instructed to give 'Remember' responses for recognized items associated with retrieval of contextual information (recollection) and give 'Know' responses when such details are lacking (familiarity). Several groups have found that 'Know' responses are associated with attenuation of the FN400 relative to correctly identified new items [correct rejections; (Curran, 2004; Duarte et al., 2004; Duzel et al., 1997)].

Indirect approaches to examining this ERP correlate have also provided data consistent with its relation to familiarity. For example, Schloerscheidt and Rugg (2004) observed the FN400 to be sensitive to stimulus format at study and test, such that change in format (e.g., picture presentation at study and name presentation at test) reduced the old/new effect. Because familiarity is postulated to be sensitive to the perceptual similarity of study and test items, or perceptual fluency (Jacoby and Whitehouse, 1989), these authors argued that this result is consistent with the relationship of the FN400 with familiarity.

Modulation of the later (500–800 ms) component of the old/new effect is often maximal over left parietal scalp sites and is frequently referred to as the LPC (late positive complex). Many studies have found modulation of the LPC with behavioral responses that are diagnostic of recollection, such as correct source or associative recognition (Curran et al., 2001; Donaldson and Rugg, 1998, 1999; Wilding and Rugg, 1996, 1997a,b). Further, studies using the Remember/Know procedure have reported a more positive LPC associated with 'Remember' compared to 'Know' responses [(Duarte et al., 2004; Duzel et al., 1997; Rugg et al., 1998b; Smith, 1993); but see Spencer et al., 2000]. Finally, factors that modulate recollection also impact LPC amplitude, such as depth of processing at encoding and word frequency (Curran, 2004; Rugg et al., 1998a).

An additional old/new ERP modulation has been described in recognition memory studies: a later, sustained potential (~600–1600 ms), that tends to be most prominent over right, frontal scalp sites (we will refer to this as the 'late frontal effect'). This modulation has been observed in a number of studies and is thought to be broadly related to post-retrieval processing (Allan and Rugg, 1997, 1998; Allan et al., 2000; Curran et al., 2001; Donaldson and Rugg, 1999; Johnson et al., 1996; Ranganath and Paller, 2000; Wilding and Rugg, 1997a,b; Wolk et al., 2004). Studies have linked this activity to evaluation of the products of retrieval for source (Wilding and Rugg, 1997b) or other item specific features (Goldmann et al., 2003; Nessler et al., 2001) and the instantiation of strategic processing related to the required task (Ranganath and Paller, 2000). Although the neural source of this signal is uncertain, it may represent prefrontally-mediated activity particularly relevant to recollection-based memory decisions (Rugg and Allan, 2000). Its contribution to familiarity is less clear, but may occur when memory decisions involve weak familiarity cues (Wolk et al., 2004, 2005). Indeed, the late frontal effect has been observed with 'Know' responses (Curran, 2004; Duzel et al., 1997; Trott et al., 1999) and may be related to the general monitoring demands of a memory task, such as when information supporting a recognition judgment is impoverished (Rugg et al., 2000, 2002).

Although the evidence supports the relationship of all three ERP correlates with their respective mnemonic functions, conflicting reports and controversies remain abundant. Such controversy has been particularly directed at the function ascribed to the FN400. For example, not all studies using the Remember/Know methodology have demonstrated a distinct ERP correlate of 'Knowing' (Smith, 1993; Trott et al., 1999). Further, some work in memory-impaired patients has failed to find a relationship between verbal memory and the related N400 while such a correlation was found with LPC modulation (Olichney et al., 2000, 2002). Because familiarity should support episodic memory, the lack of a relationship with memory performance is troubling, particularly in populations thought to be relatively dependent on familiarity-based memory (Verfaellie and Cermak, 1999; Wolk et al., 2005; Yonelinas et al., 2002; Yonelinas et al., 1998).[1]

Other studies have found that the FN400 is insensitive to manipulations that are thought to impact familiarity (Curran, 2004; Curran and Dien, 2003; Rugg et al., 1998b; Tsivilis et al., 2001). For example, Curran (2004) found no difference in FN400 attenuation for items studied in either a divided or full attention encoding task despite an increase in familiarity in the latter as estimated by the Remember/Know procedure [see (Rugg et al., 1998a) for a similar result].

Another criticism of the relationship of the FN400 with familiarity is that some studies have observed the early old/new effect to be short-lived, lasting less than 15 min (Rugg, 1990, 1995; Rugg and Nagy, 1989). Familiarity is thought to support recognition judgments for much longer retention intervals, so these results raise questions about the functional significance of the FN400. Of note, some of this work examined repetition effects rather than explicit memory (e.g., Rugg, 1990). More recent studies have reported FN400 old/new effects at more modest delays, up to 30 min (Duzel et al., 1997; Finnigan et al., 2002; Rugg et al., 1998a; Schloerscheidt and Rugg, 2004). Because recognition judgments may be associated with familiarity at study-test delays on the order of days and weeks (Gardiner and Java, 1991; Hockley and Consoli, 1999; Knowlton and Squire, 1995; Rajaram, 1993), preservation of the old/new FN400 effect at longer intervals would provide increased support for its indexing familiarity. Curran and Friedman instituted a 24-h delay between study and test phases of a picture recognition task (Curran and Friedman, 2004). They observed an FN400 old/new effect at this delay, but did not determine the nature of how the items were recognized (e.g., by recollection or familiarity). The authors argued that their finding of FN400 modulation after a prolonged retention interval, in contrast to prior results, could be explained by their use of picture stimuli as opposed to words: pictures may have enhanced the degree of familiarity of test items.

Unlike the FN400 and familiarity, the majority of studies have supported the relationship of the LPC with recollection. A few studies, however, have suggested that this modulation, or a modulation overlapping with the LPC, may be related to other factors (Finnigan et al., 2002; Johnson et al., 1985, 1998). Finnigan et al. (2002) reported reduced LPC amplitude in the setting of incorrect responses (false alarms and misses) relative to correct rejections. These authors interpreted this result as indicating that the LPC indexes accuracy and/or response confidence rather than recollection, which should have been equivalent for the incorrect responses and correct rejections. They pointed out that in much prior work only correct responses were examined resulting in a potential confound of confidence with retrieval success.

In the context of the above controversies, the present paper sought to further clarify the functional significance of the putative ERP memory correlates. Two issues were of principal importance. First, we wanted to examine further whether FN400 modulation is maintained after more extended delays (24 h) and if so, whether this modulation is associated with the feeling of familiarity. To do so, we employed the Remember/Know methodology and manipulated the interval between study and test. If FN400 modulation were maintained over the 24-h retention interval, it would be plausible that this component indexes an aspect of episodic memory (familiarity).

Second, the large number of test items employed in our experiment allowed for examination of unrelated false alarms, a class of items often neglected in previous ERP work. The main question to be answered is whether false alarms are associated with FN400 attenuation relative to correct rejections. Because familiarity is thought to drive false alarms, FN400 attenuation associated with such responses would support the relationship of the FN400 with familiarity. Indeed, Finnigan and colleagues (2002) reported an early (300–500 ms) attenuation associated with false alarms, but this study was limited by a small number of responses per individual. Further, these authors focused their analysis on posterior electrode sites, as opposed to the typical more fronto-central location of the FN400. Of the few studies that have analyzed unrelated false alarms, most have reported no difference between these responses and correct rejections (Rubin et al., 1999; Wilding and Rugg, 1996, 1997b; Wilding et al., 1995). By examining false alarm ERPs formed by a relatively large number of trials, the present report sought to clarify this issue.[2] An additional benefit of studying memory errors, such as false alarms, is to determine whether such inaccuracy is associated with modulation of the LPC, as reported by Finnigan et al. (2002). If unrelated false alarms, responses

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[1] It is worth noting that Olichney and colleagues examined the N400 semantic congruity effect rather than the FN400 old/new effect.

[2] In contrast to the limited number of studies examining unrelated false alarms, as noted above there has been a fairly extensive literature focused on false alarms to semantically- or perceptually-related, non-studied items (Curran, 2000; Curran and Cleary, 2003; Curran et al., 2001; Goldmann et al., 2003; Nessler et al., 2001). Such false alarms differ from those to unrelated items as they appear to be at least partially driven by recollection, as marked by their frequent association with 'Remember' responses (Roediger and McDermott, 1995); however, the ERP literature has been mixed in support of the association of related false alarms with recollection, as measured by LPC modulation. Nonetheless, for this reason related false alarms may be less informative than unrelated false alarms in isolating the neural basis of familiarity.

thought devoid of recollection, are associated with LPC modulation, this would have important functional implications for this component. A larger amplitude LPC for false alarms than correct rejections would support the relationship of this component to explicit 'memory', but may suggest that it is in part modulated by familiarity, as unrelated false alarms would not be expected to be frequently associated with recollection. Alternatively, a smaller amplitude LPC for false alarms compared to correct rejections may suggest sensitivity to accuracy or confidence related factors.

2. Results

2.1. *Behavioral data*

Collapsed across the one- and three-presentation conditions, both groups were more likely to endorse studied items as 'Old' than non-studied items (Table 1). Both groups produced a similar proportion of correctly recognized studied items, as well as a similar proportion of 'Remember' and 'Know' responses. False alarms were higher in the long-delay group suggesting overall reduced discrimination compared to the short-delay group. Both groups more often produced 'Remember' than 'Know' responses for studied items endorsed as 'Old'; however, the majority of false alarms were associated with 'Know' responses.

For analysis of the behavioral data, studied items were collapsed over the one- and three-presentation conditions (the same was done for the ERP data because the correlates of memory retrieval were of primary interest, not the nature of encoding). A delay (short-delay, long-delay) × study status (studied, non-studied) ANOVA revealed a main effect of study status [$F(1,25) = 179.9$; $P < 0.001$, $\eta^2 = 0.88$] with studied items called 'Old' much more frequently than non-studied items (0.81 versus 0.38) and a delay by study status interaction [$F(1,25) = 7.05$; $P = 0.014$, $\eta^2 = 0.22$]. The latter interaction occurred because false alarms were greater in the long-delay than short-delay group [$t(25) = 2.09$, $P = 0.047$] while hits ('Old' endorsements of studied items) did not differ [$t(25) < 1$]. Hit-'Remember' and hit-'Know' responses did not differ between the two delays [ts < 1] while there were trends for both false alarm-'Remember' and false alarm-'Know' responses to be greater in the long delay group [false alarm-'Remember': $t(25) = 1.83$, $P = 0.079$; false alarm-'Know': $t(25) = 1.72$, $P = 0.099$].

To determine whether hit-'Remember' and hit-'Know' responses differed in the delay conditions based on the proportion of responses associated with the one- and three-presentation study items, we compared the proportion of three-presentation items contributing to both response types. Both groups had a greater proportion of hit-'Remember' responses associated with the three-presentation than one-presentation condition, but this proportion did not differ across delay [.65 (short-delay) versus 0.62 (long-delay); $t(25) = 1.41$, $P > 0.1$]. As might be expected, a numerically greater proportion of hit-'Know' responses were from the three-repetition study condition in the long- versus short-delay groups (0.45 versus 0.38, respectively). However, this difference was also not statistically significant ($t(25) = 1.61$, $P > 0.1$). The lack of significant differences in these proportions further supports the collapsing of this ERP data across repetition in the short- versus long-delay comparison (Fig. 1).

Table 1 – Mean proportion of response types

	Studied	Non-studied
Short-Delay		
'Old'	0.82 (0.03)	0.31 (0.05)
'Remember'	0.52 (0.05)	0.06 (0.02)
'Know'	0.30 (0.03)	0.25 (0.04)
Long-Delay		
'Old'	0.79 (0.03)	0.45 (0.04)
'Remember'	0.47 (0.05)	0.11 (0.02)
'Know'	0.32 (0.03)	0.33 (0.03)
Combined Delay Conditions		
'Old'	0.81 (0.02)	0.38 (0.04)
'Remember'	0.50 (0.03)	0.08 (0.02)
'Know'	0.31 (0.02)	0.29 (0.03)

SEM in parentheses.

2.2. *ERP analysis*

2.2.1. *'Remember', 'know', and correct rejections*

As can be seen in Figs. 2 and 3, 'Remember' and 'Know' responses for hits, collapsed over the two delay conditions, appear to be associated with attenuation of the FN400 relative to correct rejections. This attenuation is present in both the short-delay and long-delay conditions (see Fig. 5). Only 'Remember' responses are associated with an increased LPC and a right hemisphere late frontal effect.

2.2.1.1. *300–500 ms (FN400).*

'Know' versus correct rejections. A delay (short, long) × response ('Know', correct rejections) × a–p (anterior–posterior; prefrontal, frontal, central, parietal, occipital) × laterality (left outer lateral, left inner lateral, midline, right inner lateral, right outer lateral) ANOVA revealed a main effect of response [$F(1,25) = 14.21$, $P = 0.001$, $\eta^2 = 0.36$], indicating that the 'Know' responses were more positive than correct rejections (attenuation of FN400). This effect was modulated by factors of a–p [$F(4,100) = 5.77$, $P = 0.012$], laterality [$F(4,100) = 3.76$, $P = 0.022$], and a–p × laterality [$F(16,400) = 2.49$, $P = 0.016$], as the effect of response appeared largest at midline and centro-parietal sites (Fig. 4). Importantly, there were no interactions with delay, including delay × response [$F(1,25) = 1.75$, $\eta^2 = 0.07$].

'Remember' versus correct rejections. The analogous ANOVA produced a main effect of response [$F(1,25) = 6.59$, $P = 0.017$, $\eta^2 = 0.21$], indicating that 'Remember' responses were more positive than correct rejections. This main effect interacted with a–p [$F(4,100) = 3.98$, $P = 0.031$], as the effect of response appeared largest at prefrontal and frontal locations (see Fig. 4).

'Remember' versus 'know'. There was no main effect of response [$F(1,25) < 1$, $\eta^2 = 0.02$], nor significant interaction of response with any factor. However, there was a trend for a response × delay interaction [$F(1,25) = 3.48$, $P = 0.074$, $\eta^2 = 0.12$]: 'Know' responses tended to be more positive than the 'Remember' responses in the short-delay group while the

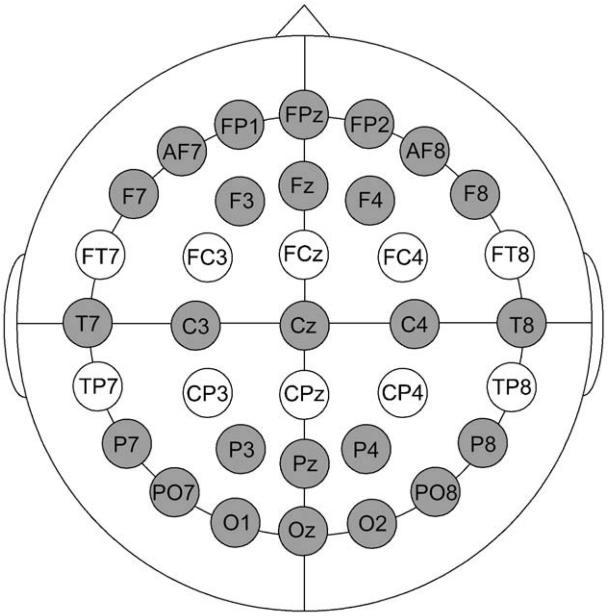

Fig. 1 – Scalp Site Array. Shaded sites show scalp locations for electrodes used in analysis.

opposite pattern was found in the long-delay group. This trend toward an interaction was further examined with separate response × a–p × laterality ANOVAs for both delay conditions. A main effect approached significance in the short-delay group [$F(1,13) = 3.39$, $P = 0.088$, $\eta^2 = 0.21$], but was not significant in the long-delay group [$F(1,12) < 1$, $\eta^2 = 0.05$]. The near significant effect in the short-delay group appeared to be driven by more positive 'Know' responses than 'Remember' responses, particularly at posterior sites, as reflected by a response × a–p interaction [$F(4,52) = 6.43$, $P = 0.005$]. This interaction also reached significance in the long-delay condition [$F(4,48) = 5.66$, $P = 0.031$], with 'Know' responses showing greater amplitude than 'Remember' responses at posterior sites, but the opposite pattern more anteriorly.

Comparisons at Fz. Given the prior literature suggesting an anterior distribution of the familiarity correlate (Curran and Cleary, 2003; Nessler et al., 2001; Rugg et al., 1998a), planned comparisons were performed at Fz, the site where this effect is most often maximal. For each comparison a response × delay (short, long) ANOVA was performed. Both 'Know' [$F(1,25) = 11.84$, $P = 0.002$, $\eta^2 = 0.32$] and 'Remember' [$F(1,25) = 10.59$, $P = 0.003$, $\eta^2 = 0.30$] responses were more positive (attenuated FN400) than correct rejections. Importantly, neither of these effects was modified by delay [$Fs < 1$, $\eta^2\mathrm{s} < 0.02$; Figs. 5 and 6]. 'Know' and 'Remember' responses did not differ [$F(1,25) < 0.01$, $\eta^2 < 0.01$].

2.2.1.2. *500–800 ms (LPC)*.

'Know' versus correct rejections. There was no main effect of response [$F(1,25) < 1$, $\eta^2 = 0.01$] or interaction of response with any other factors, including delay [$F(1,25) < 0.1$, $\eta^2 < 0.01$].

'Remember' versus correct rejections. There was a main effect of response [$F(1,25) = 10.32$, $P = 0.004$, $\eta^2 = 0.29$], indicating that 'Remember' responses were associated with an increased amplitude relative to correct rejections. The effect of response was not modified by delay [$F(1,25) < 1$, $\eta^2 < 0.01$; see Figs. 5 and 6]. Response × laterality [$F(4,100) = 4.48$, $P = 0.010$] and response × a–p × laterality [$F(16,400) = 3.46$, $P = 0.002$] interactions were significant, likely because of a right hemisphere maximal effect at anterior sites and a more bilaterally distributed effect at posterior sites (Fig. 4).

'Remember' versus 'know'. Similar results were obtained with comparison of 'Remember' to 'Know' responses as

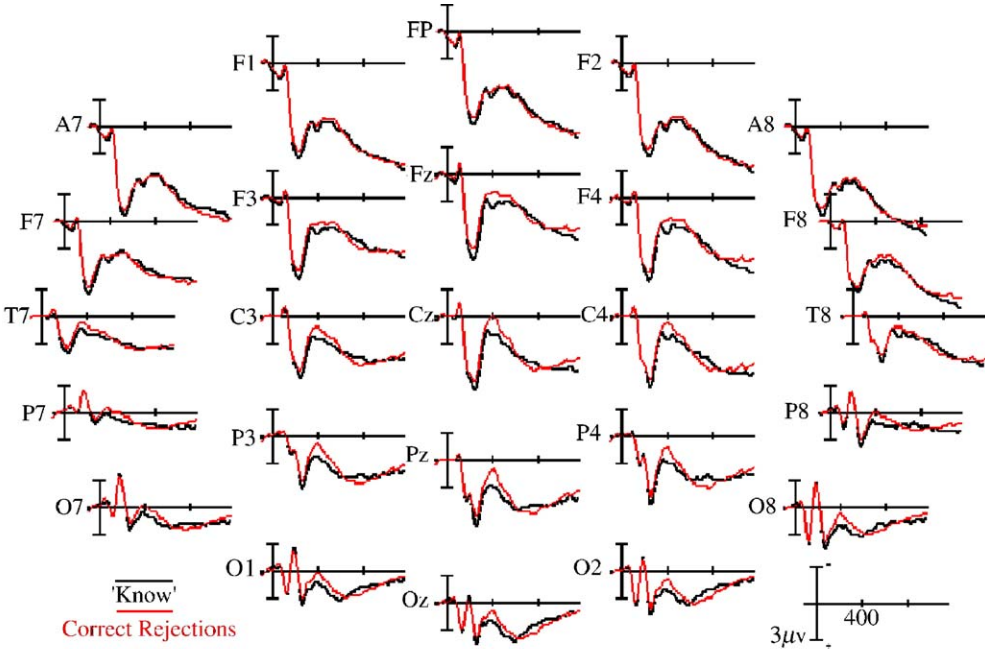

Fig. 2 – 'Know' Responses Versus Correct Rejections. Grand average ERP plots for 'Know' (black) and correct rejections (red) collapsed over both the short- and long-delay conditions.

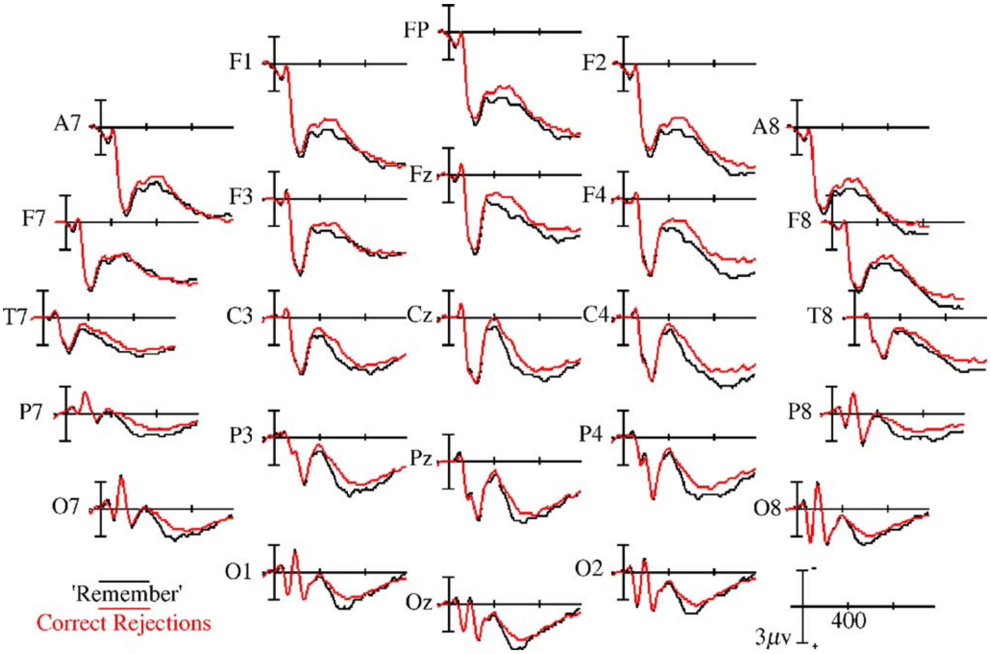

Fig. 3 – 'Remember' Responses Versus Correct Rejections. Grand average ERP plots for 'Remember' (black) and correct rejections (red) collapsed over both the short- and long-delay conditions.

with 'Remember' to correct rejections. A main effect of response was significant [F(1,25) = 19.344, $P < 0.001$, $\eta^2 = 0.44$] due to a larger amplitude associated with 'Remember' than 'Know' responses. Similar to the 'Remember' versus correct rejections distribution, this effect was modified by a significant interaction with laterality [F(4,100) = 5.09, $P = 0.008$] and a trend towards an interaction with a–p × laterality [F(16,400) = 1.71, $P = 0.16$]. Again, there were no interactions with delay, including delay × response [F(1,25) < 0.1, $\eta^2 < 0.01$].

Comparisons at P3. Prior literature has frequently reported the LPC repetition effect to be maximal at left parietal scalp sites. In this context, planned comparisons were pursued with response × delay (short, long) ANOVAs at P3. 'Remember' responses were more positive than both 'Know' responses [F(1,25) = 14.71, $P = 0.001$, $\eta^2 = 0.37$] and correct rejections [F(1,25) = 7.908, $P = 0.009$, $\eta^2 = 0.24$]. In neither case did this effect interact with delay [F(1,25) < 0.1, $\eta^2 < 0.01$ and F(1,25) < 1, $\eta^2 = 0.02$, respectively]. There was no difference between 'Know' responses and correct rejections [F(1,25) < 0.1, $\eta^2 = 0.01$].

2.2.1.3. 800–1170 (Late frontal effect).

'Know' versus correct rejections. There was no main effect of response [F(1,25) < 1, $\eta^2 < 0.01$]. However, a condition × a–p × laterality interaction reached significance [F(16,400) = 2.45, $P = 0.013$], likely because of a tendency for 'Know' responses to be more positive over right frontal and central scalp sites (Fig. 4). This interaction was not further modified by delay [F(16, 400) < 1, $\eta^2 = 0.03$].

'Remember' versus correct rejections. Although there was only a trend toward a main effect of response [F(1,25) = 3.64, $P = 0.068$, $\eta^2 = 0.13$], the critical interactions of response × laterality [F(4,100) = 6.44, $P = 0.001$] and response × a–p × laterality [F(16,400) = 3.62, $P = 0.001$] were significant. Additionally, the response × a–p interaction approached significance [F(4,100) = 2.96, $P = 0.068$]. These interactions appeared the result of the effect of response ('Remember' > correct rejections) being largest at anterior, right hemisphere scalp sites (see Fig. 4). These interactions were not modified by delay [response × a–p × delay: F(4,100) < 1, $\eta^2 = 0.01$; response × laterality × delay: F(4,100) = 1.038, $\eta^2 = 0.11$; response × a–p × laterality × delay: F(16,400) < 1, $\eta^2 = 0.01$]. The delay × response interaction also was not significant [F(1,25) = 2.17, $P = 0.154$, $\eta^2 = 0.08$]; however, 'Remember' responses tended to be of larger amplitude relative to correct rejections in the long compared to the short-delay condition (see Fig. 5).

'Remember' versus 'know'. A main effect of response [F(1,25) = 3.48, $P = 0.074$, $\eta^2 = 0.12$] and a response × laterality interaction [F(4,100) = 2.601, $P = 0.073$] approached significance. 'Remember' responses tended to be more positive than 'Know' responses, particularly over right hemisphere scalp sites. No other interactions with response were significant.

Comparisons at F4. The above omnibus ANOVAs suggest that modulation of the late effect was most prominent at right hemisphere, frontal scalp sites. This result is also consistent with prior ERP memory studies. To specifically examine this region, planned comparisons were performed at F4 with response × delay (short, long) ANOVAs. 'Remember' responses were associated with a more positive amplitude than correct rejections [F(1,25) = 17.46, $P < 0.001$, $\eta^2 = 0.41$]. Although the magnitude of this effect was greater in the long-delay condition, the response × delay interaction was not significant [F(1,25) = 2.12, $P = 0.158$, $\eta^2 = 0.08$]. 'Remember' responses were also more positive than 'Know' responses [F(1,25) = 7.45, $P = 0.011$, $\eta^2 = 0.23$], but 'Know' responses did not significantly differ from correct rejections [F(1,25) = 2.03, $P = 0.166$, $\eta^2 = 0.08$].

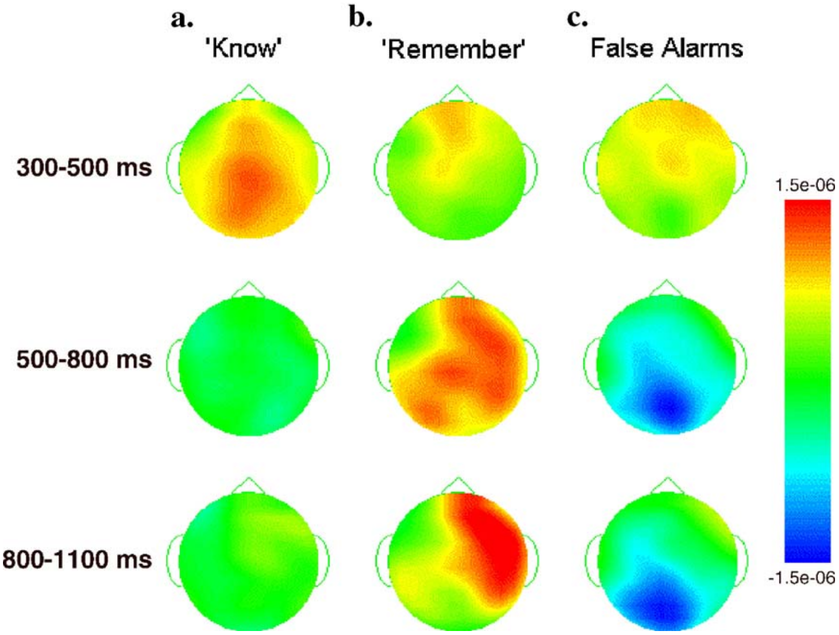

Fig. 4 – Topographic Distributions. Topographic distribution of ERP differences between (a) 'Know' (b) 'Remember', and (3) false alarms minus correct rejections. Each are shown at the three intervals of interest.

Neither of these latter two comparisons interacted with delay [Fs < 1].[3]

2.2.2. *False alarms and correction rejections*

Fig. 7 displays the ERPs for false alarms and correct rejections collapsed across the short- and long-delay conditions. As can be seen, false alarms are associated with attenuation of the FN400 relative to correct rejections, consistent with the notion that such errors are associated with familiarity. In addition, decreased amplitude is seen with false alarms compared to correct rejections in the temporal epoch of the LPC, but perhaps extending beyond it.

2.2.2.1. 300 – 500 ms (FN400). As with the above analyses, a delay (short, long) × response (false alarms, correct rejections) × a–p (prefrontal, frontal, central, parietal, occipital) × laterality (left outer lateral, left inner lateral, midline, right inner lateral, right outer lateral) ANOVA was calculated. This revealed a main effect of response, such that false alarms had a more positive amplitude (attenuated FN400) than correct rejections [$F(1,25) = 7.66$, $P = 0.010$, $\eta^2 = 0.24$]. There were no interactions with this effect, including with delay [$F(1,25) < 0.1$, $\eta^2 < 0.01$]. As with the FN400 analysis above, a planned comparison was calculated at Fz with a response × delay ANOVA. Consistent with the omnibus ANOVA, false alarms were associated with a more positive amplitude at Fz than correct rejections [$F(1,25) = 6.06$, $P = 0.021$, $\eta^2 = 0.20$]. It is worth pointing out that although false alarms were somewhat less positive at Fz than 'Remember' and 'Know' responses [3.25 μV versus 3.51 μV and 3.46 μV, respectively], these responses did not statistically differ [Fs < 1].

2.2.2.2. 500 – 800 ms (LPC). Given the notion that false alarms would be driven by familiarity, we were primarily interested in the effect of such responses on the FN400. However, there was a clear modulation seen in the temporal epoch of the LPC. To analyze this effect, the analogous omnibus ANOVA was performed.[4] A near significant main effect of response was observed [$F(1,25) = 3.82$, $P = 0.062$, $\eta^2 = 0.13$] due to correct rejections having a more positive amplitude than false alarms. Additionally, response × a–p [$F(4,100) = 6.03$, $P = 0.006$], response × laterality [$F(4,100) = 4.91$, $P = 0.005$], and response × a–p × laterality [$F(16,400) = 3.147$, $P = 0.003$] interactions were significant. These interactions appeared driven by the effect of response being maximal at midline and parietal scalp sites (see Fig. 4). Although there was not a response × delay interaction [$F(1,25) = 1.14$, $P = 0.30$, $\eta^2 = 0.04$], the response × laterality interaction was modified by delay [$F(4,100) = 2.93$, $P = 0.044$, $\eta^2 = 0.11$], as the magnitude of this interaction was smaller in the long-delay group. As with the other analyses in this temporal window, a more focused response × delay ANOVA was calculated for the P3 scalp site. Consistent with the above omnibus ANOVA, this revealed a main effect of response [$F(1,25) = 9.69$, $P = 0.005$, $\eta^2 = 0.28$], such that false alarms had a smaller amplitude than correct rejections. There was no interaction with delay [$F(1,25) < 1$, $\eta^2 = 0.03$].

3. Discussion

The current study examined three ERP modulations thought to relate to different aspects of recognition memory.

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[3] Of note, direct comparisons at F4 across delay conditions for 'Remember', 'Know', and correct rejections did not reveal significant differences (ts < 1).

[4] Note that nearly identical results were obtained in analysis of the 800–1170 ms interval, suggesting this effect was not limited to the typical epoch of the LPC (also see Fig. 4). These results are not presented here for brevity.

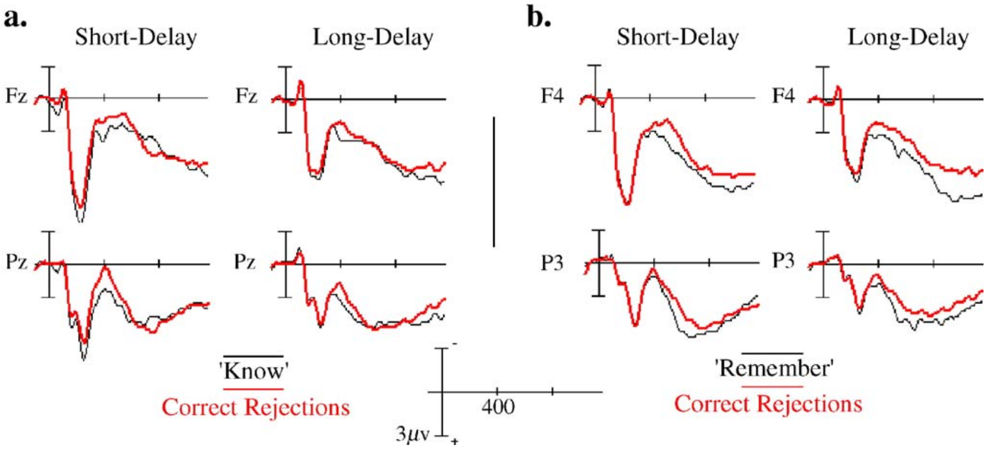

Fig. 5 – Responses by Delay Condition. Grand average ERP plots at select sites comparing short- and long-delay conditions. (a) 'Know' (black) and correct rejections (red) at two midline sites to best capture FN400 effect. (b) 'Remember' (black) and correct rejections (red) at P3 and F4 to best capture LPC and late frontal effect, respectively.

Correlates of 'Remember' and 'Know' responses appeared relatively stable over a 24-h delay, suggesting that the neural underpinnings of these introspectively determined mnemonic states are essentially unchanged over this period. The consistent mapping of these phenomena to specific neural events demonstrates that the criteria used by subjects to make these decisions is relatively robust. In addition to investigating the impact of study-test delay on these ERP correlates, we also obtained a sufficient number of unrelated false alarms to examine this often-neglected response category. ERP modulation of such responses has important implications for the functional significance of the putative mnemonic correlates. With respect to the current data, we will discuss the FN400, LPC, and late frontal effects in turn.

3.1. FN400

Several lines of evidence in the current data support the assertion that the FN400 indexes familiarity. First, consistent with other studies using the Remember/Know paradigm (Curran, 2004; Duarte et al., 2004; Duzel et al., 1997), 'Know' responses were associated with FN400 attenuation relative to correct rejections. Such responses are thought to represent recognition based purely on familiarity. As such, this finding adds to a growing literature in which familiarity-based responses appear associated with FN400 modulation (Curran, 2000; Curran and Cleary, 2003; Curran et al., 2002; Nessler and Mecklinger, 2003; Nessler et al., 2001). The variety of ways that familiarity was operationalized in these studies supports the generality of this relationship.

Second, in the current paradigm, we found that modulation of the FN400 was maintained after a 24-h retention delay. This result answers the criticism that the early (300–500 ms) old/new modulation is too short-lived to be a plausible correlate of familiarity and, instead, reflects a short-term memory process (Olichney et al., 2000; Rugg, 1995). Our finding confirms a recent study by Curran and Friedman (2004) in which they also observed an FN400 old/new effect after a 24-h delay. These authors suggested that their use of pictures as stimuli may explain the persistence of this effect relative to prior studies in which words were used (Rugg, 1990; Rugg and Nagy, 1989). They speculated that the use of picture stimuli may have reduced the forgetting rate relative to words. Our results extend Curran and Friedman's findings by demonstrating a maintained FN400 modulation for words after a 24-h delay. Further, this effect appeared specifically related to item familiarity ('Know' responses). The discrimination (hits-false alarms) of our long-delay group (34%) was significantly lower than that of Curran and Friedman (77%). Thus, even in the setting of relatively poor discrimination (a high forgetting rate), a persistent FN400 modulation was observed.

Third, false alarm responses were associated with FN400 modulation. False alarms to unrelated items are likely driven by familiarity, as evidenced by their association with a much higher rate of 'Know' than 'Remember' responses. Such a result is consistent with models of familiarity described by signal detection theory in which false alarms are driven by familiarity that exceeds the threshold for endorsing an item as 'Old' (Curran, 2004; Finnigan et al., 2002; Yonelinas, 2001, 2002). Few ERP studies have closely examined false alarms to unrelated items. Most prior work has focused on false alarms to semantically- or perceptually-related, non-studied items. These studies have frequently reported FN400 attenuation (Curran, 2000; Curran and Cleary, 2003; Nessler et al., 2001) and, in some, increased LPC voltage (Curran et al., 2001; Goldmann et al., 2003; Nessler et al., 2001) consistent with the notion that related false alarms may be associated with recollection.

Although a few studies have reported no difference between unrelated false alarms and correct rejections (Rubin et al., 1999; Wilding and Rugg, 1996, 1997b; Wilding et al., 1995), the current result is similar to that reported by Finnigan and colleagues (2002) in which an early (300–500 ms) attenuation was found with false alarms (analyzed at P3). These authors noted that on examination of some reports in the extant literature there appears to be similar attenuation with false alarm responses, even if not analyzed or reported [for example, see (Van Petten and Senkfor, 1996)]. It is worth pointing out that Finnigan and colleagues attributed this modulation to a strength-based memory process, akin to

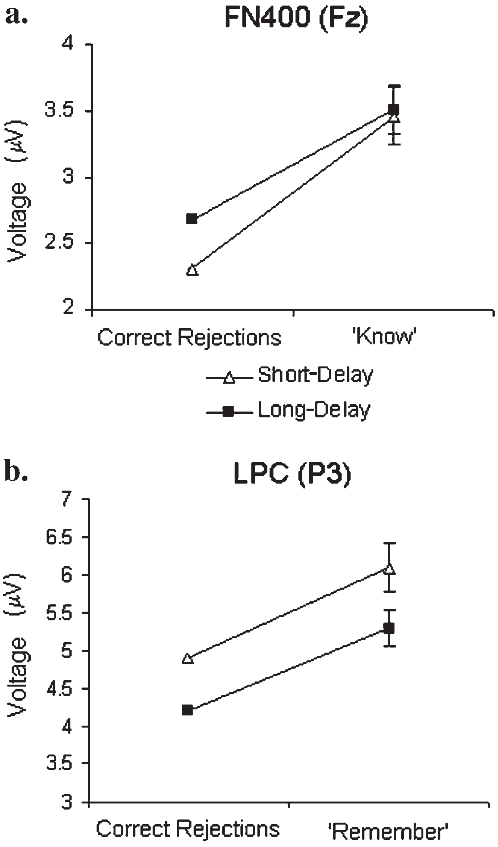

Fig. 6 – FN400 and LPC by Delay. Mean amplitudes of the (a) FN400 and (b) LPC for both delay conditions. The FN400 is measured by the mean amplitude from 300 to 500 ms at Fz for 'Know' responses and correct rejections. The LPC is measured by the mean amplitude from 500 to 800 ms at P3 for 'Remember' responses and correction rejections. Error bars represent the standard error of the 'old/new' difference (accounting for absence of error bars for correct rejections).

familiarity, but in the context of a single-process model. Importantly, the Finnigan et al. (2002) result should be interpreted with caution given the relatively low number of false alarm responses from which ERPs were formed (mean = 11.78). Replication with the present dataset in which the average number of false alarm trials used to generate ERPs was much higher (mean = 105.2) provides additional support for their finding. Taken together, the present data suggest that FN400 modulation is related to the feeling of familiarity regardless of the prior study history of an item.

A relevant question is what drives the increased familiarity of the non-studied items to which subjects false alarm. While the current study does not address this issue, one speculation is that these items are familiar because they are more semantically related to other words in the study list than the correctly rejected non-studied items. This relatedness would increase the semantic fluency of these items resulting in greater familiarity. The attenuation of the FN400 may reflect this enhanced fluency, just as semantic priming produces N400 attenuation in studies of language (Holcomb, 1993; Kutas and Hillyard, 1980; Rugg and Doyle, 1994). A related possibility is that the false alarms tend to be words that are more frequent in the lexicon, or perhaps more familiar to a given individual. Indeed, much work has supported that higher frequency words are more likely to produce false alarms than lower frequency ones (Arndt and Reder, 2002; Balota et al., 2002). Word-frequency effects have been shown to modulate N400 amplitude with greater attenuation associated with higher frequency words (Young and Rugg, 1992). In the context of a recognition memory test, such attenuation could produce a 'false' sense of familiarity leading to false alarms. Detailed investigation of the semantic properties of false alarms and how the relate to electrophysiology would provide increased insight into this issue.

It is worth noting the scalp topography of the 'Remember', 'Know', and false alarm conditions relative to correct rejections (see Fig. 5). In addition to the fronto-central FN400 effect, a positive voltage was observed at posterior sites in the 300–500 ms interval for 'Know' responses relative to correct rejections. It has been argued that this posterior modulation is a correlate of an implicit repetition effect while the anterior modulation is associated with familiarity [e.g., Rugg et al. (1998a)]. Thus, it is not surprising that false alarms, items which were not previously presented, would not produce this posterior modulation. On the other hand, it is unclear why such an effect was not present with 'Remember' responses.

3.2. LPC

Consistent with prior work, 'Remember' responses were associated with a more positive LPC than correct rejections and 'Know' responses (Curran, 2004; Duarte et al., 2004; Duzel et al., 1997; Rugg et al., 1998b). This LPC effect was more symmetric at posterior sites than often reported, but this may be due to overlap with the right hemisphere effect which had a similar temporal onset, but more extended course (see Fig. 4). That 'Know' responses did not differ from correct rejections supports the notion that the LPC specifically indexes recollection. However, the data from false alarms present a challenge to this formulation. False alarms were associated with a decreased amplitude of the LPC relative to correct rejections. Because neither of these responses should be associated with recollection, this result appears to be inconsistent with the notion that the LPC simply reflects recollection.

An alternative view is that the LPC may be sensitive to other response-related characteristics, such as confidence or accuracy (Finnigan et al., 2002; Johnson et al., 1985, 1998). The current data are very similar to what was reported by Finnigan and colleagues (2002). They found that false alarms (and misses) were associated with a smaller LPC amplitude than correct rejections. These investigators argued that based on this result the LPC cannot be ascribed to recollection, but possibly indexes decisional factors, such as accuracy and/or confidence.

Another possibility is that the LPC modulation seen in the current data is due to overlapping ERP components. A posterior negativity has been described in a few false memory paradigms, specifically in association with false alarms to related lures (Curran, 2000; Johnson et al., 1997; Nessler and Mecklinger, 2003; Nessler et al., 2001). Although the onset of the current effect was earlier than reported in these studies (approximately 550 ms versus 700–800 ms), the sustained

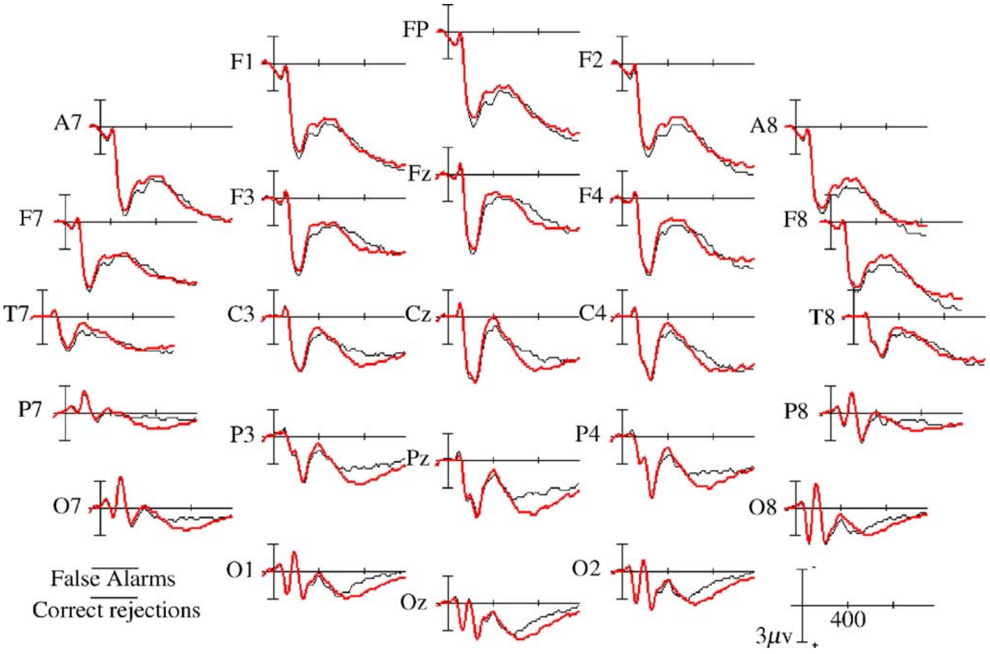

Fig. 7 – False Alarms Versus Correct Rejections. Grand average ERP plots for false alarms (black) and correct rejections (red) collapsed over both the short- and long-delay conditions.

nature of this modulation beyond the typical LPC offset (near the end of the recording epoch; see Fig. 4) is consistent with these previous reports. Additionally, the present false alarm versus correct rejection effect appeared of a somewhat later onset than the LPC effect seen with 'Remember' responses (see Figs. 3 and 7). Johansson and Mecklinger (2003) speculated that this activity may reflect response conflict or action monitoring. Indeed, when Nessler et al. (2001) divided subjects into those with high and low levels of false alarms, they found that the false alarm/correct rejection voltage difference was larger in the low false alarm group. These authors argued that this finding was consistent with the notion that this effect indexes response conflict, as false alarms may be associated with greater conflict in the group less likely to commit such errors. It is worth pointing out that the difference in false alarm rate between the two groups may have resulted in differential signal-to-noise ratios for both correct rejections and false alarms, which may have contributed to the observed finding. Nonetheless, if the results of the present study represent the same 'posterior negativity', this would extend the finding to false alarms in 'classic' recognition memory paradigms (e.g., not involving related, non-studied lures) and would suggest that this effect may be generally related to response conflict.

3.3. *Late frontal effect*

As reported in a number of studies, we found a sustained anterior effect, which was maximal at right hemisphere scalp sites. That this modulation was most prominent for 'Remember' responses is consistent with the notion that this activity represents prefrontal processing related to tasks involving recollection. For example, other work has found this effect most prominent in tasks involving source judgments, cued recall, or when items need to be distinguished on the basis of specific features [e.g., tasks involving recollection; (Allan and Rugg, 1998; Allan et al., 2000; Curran et al., 2001; Donaldson and Rugg, 1998; Goldmann et al., 2003; Rugg et al., 1998b; Wilding and Rugg, 1996)].

However, other studies using the Remember/Know paradigm have reported equivalent late frontal activity associated with both 'Remember' and 'Know' responses (Curran, 2004; Duzel et al., 1997; Trott et al., 1999). These data, in combination with results from other ERP and fMRI memory paradigms, has led to the suggestion that recollection is neither necessary nor sufficient for such prefrontal activation, but that this activity is instantiated in situations in which large demands are placed on post-retrieval monitoring related to the memory task (Rugg et al., 2000, 2002). Based on this logic, the equivalence of the late frontal effect in prior studies for both 'Remember' and 'Know' responses may reflect that such introspective decisions require similar monitoring.

Thus, the specificity of the late frontal effect to 'Remember' responses in the current data contradicts these prior Remember/Know ERP studies and the notion that the effect purely reflects monitoring demands. There are several important differences between this and the previous studies. Most importantly, the current paradigm consisted of a two-step process in which subjects first made an 'Old/New' decision and then a 'Remember/Know' judgment. In contrast, the studies of Duzel and colleagues and Curran required a single-step 'Remember/Know/New' decision. This single decision may have confounded prefrontal processing related to determining the nature of the perceived 'oldness' of the item with processing related specifically to recollection-based retrieval. Further, in the study by Duzel et al., subjects had to discriminate studied items from semantically-related non-studied lures, increasing the monitoring demands of all test items. Another important issue is that the intervals examined by Curran and Duzel et al. were later than that of the current study (1000–1500 ms and 1300–1900 ms, respectively). Thus, it is unclear whether we would have seen equivalence in the late frontal effect for 'Remember' and 'Know' responses if the recording epoch were longer. Nonetheless, these prior studies did not reveal the 'Remember' greater than 'Know' effect overlapping with the interval examined here (800–1170 ms).

As with the current paradigm, Trott and colleagues utilized a two-step decision process (the interval examined, 830–1450 ms, overlapped with the present one to a greater extent than the above two studies). Although they reported that the late frontal activity was not significantly different for 'Remember' and 'Know' decisions, in examining their data (Fig. 2), 'Know' responses appeared less positive than 'Remember' responses at F4 and no different from new items. Only at a site above the right eye were 'Know' and 'Remember' responses equivalent. Thus, the present data, along with Trott et al., suggest that some aspect of this prefrontal processing is specific to recollection-based retrieval. This result may be integrated with other accounts by proposing that the right frontal effect encompasses several different retrieval-related functions and, thus, may be linked to increased monitoring demands and effort, as well as to successful retrieval and evaluation of recollected material.

Indeed, the magnitude of the late frontal effect was larger (although not statistically so) in the long-delay relative to short-delay condition for 'Remember' responses relative to correct rejections, possibly related to increased retrieval effort or monitoring demands required with the longer retention interval. However, the magnitude of this difference across delay condition for 'Know' responses relative to correction rejections did not approach a statistical effect (although the effect was also marginally larger in the long delay condition). While the lack of a more robust late frontal effect related to retention interval might suggest that the impact of relative retrieval demands is not a potent modulator of this effect, several caveats should be mentioned. First, the differential in the difficulty of the compared memory tasks, which impacts the richness of the retrieved information and monitoring demands, is likely to be critical to the degree to which the late frontal effect varies. For example, Li and colleagues found no difference in the late frontal effect for items studied once versus items studied twice in a source memory task (Li et al., 2004). Importantly, both item and source memory were only modestly affected by the encoding condition (0.03 and 0.07, respectively). In contrast, Rugg et al. (2000) found a larger late frontal old/new effect for words studied in a shallow versus deep encoding task in which item discrimination was markedly different (0.51). Despite the 24-h delay, the discrimination (hits-false alarms) difference across the two retention intervals in the present study was modest (0.17), which may account for the effect of delay not reaching significance. Second, the criteria by which participants would be willing to endorse an item as a 'Remember' or 'Know' response may have been similar regardless of the delay condition. In fact, the lack of difference in the FN400 and LPC old/new effects across the retention intervals for these response types is consistent with this notion. As such, it would not be expected that the strength of the memory trace would vary significantly enough to result in a greater depth of post-retrieval processing for a given response across the delay conditions. Finally, as noted above, some have found frontal effects with a later onset than investigated here, and it is possible that a longer recording epoch would have allowed for observance of a larger effect of delay on this activity. Nonetheless, to our knowledge, this is the first ERP study comparing late frontal old/new effects over such a long study-test delay.[5] More intensive investigation of the effect of varying retention interval on this late frontal modulation designed to account for the above caveats would be informative with regard to the hypothesized role of this neural activity.

3.4. *Conclusion*

The present study adds further support to the notion that the FN400 is related to familiarity and the late right frontal effect to recollection. However, examination of false alarms casts some doubt as to whether modulation within the typical LPC interval purely reflects recollection of study details. Instead, this modulation, or, more likely, an overlapping posterior negativity, may be sensitive to decision-related factors, such as response conflict, confidence, or accuracy. Further investigation in which such factors are systematically manipulated will add to understanding of this 'old/new' effect.

4. Experimental procedures

4.1. *Subjects*

Informed consent was obtained from 31 healthy, right-handed students at Harvard University (18 female; mean age: 20.5 years; range: 18–22 years). Sixteen subjects participated in a single session in which the test phase followed the study phase after a short delay. The remaining fifteen subjects completed study and test phases in two sessions separated by approximately 24 h. Data from 4 subjects (two from both the short-delay and long-delay condition) were not included due to computer malfunction during ERP recording or inadequate behavioral performance. Participation was voluntary and subjects were compensated $25 per hour. The study was approved by the human subjects committee of Brigham and Women's Hospital, Boston, MA.

4.2. *Materials and design*

Stimuli consisted of 600 words (4 to 8 letters; mean Kucera–Francis frequency: 155.2; mean Kucera–Francis familiarity:

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[5] Curran and Friedman examined late frontal old/new effects (800–1800 ms) in a task in which one group of participants studied two lists of items, one just prior to test and the other 24 h prior to the test phase. A second group studied both lists on the same day. However, they only compared old/new effects across the two groups for test items from the list studied on the same day as the test phase (Curran and Friedman, 2003).

561) collected from the University of Western Australia MRC Psycholinguistic database (http://www.psy.uwa.edu.au/MRCDataBase/UWA_mrc.htm). Words were divided into four lists of 150 words. Study lists were made up of two of these four lists. One set of 150 words was presented once in the study phase while the other was presented three times. Based on pilot data, the three-presentation condition was used to ensure an adequate number of 'Remember' responses at test in the long delay condition to produce reliable ERPs. Likewise, the one-presentation condition was used to ensure an adequate number of 'Know' responses in the short-delay condition. The order of presentation was pseudo-randomized such that no word was presented more than once within 10 stimuli. For the test phase, all 600 words were presented (300 studied; 300 non-studied). Test order was pseudo-randomized with no more than three words of a particular study status presented in sequence. A total of four counter-balanced study-test lists were created, such that each word list served once as a single-presentation study item, once as a three-presentation study item, and twice as a non-studied test item.

4.3. *Procedure*

Subjects were told that their participation would involve either one or two sessions. To produce the same study environment for both groups (short-delay; long-delay), face electrodes and the elastic cap (see below) were placed on all subjects prior to the study phase. Subjects were not explicitly told that the task was a memory test. For each study word, subjects were asked to rate it as "pleasant" or "unpleasant" based on their experience (for example, if the word were "Dog", the subject may rate it as pleasant because they have a pet dog). The task was self-paced and the word would remain on the screen until the subject entered a response with a button press on a controller. Each response was followed by a 500-ms fixation '+' prior to presentation of the next study item.

Prior to the test phase, subjects read detailed instructions outlining the test procedures and the Remember/Know distinction. These instructions were adapted from prior studies using this methodology (Gardiner, 1988; Rajaram, 1993). To ensure that the subjects understood these instructions, they were asked to explicitly discuss how they would make the distinction between 'Remember' and 'Know' responses. Based on this discussion, the examiner would provide further instruction or proceed to the test phase.

Each test word was presented after a 500-ms fixation '+'. The test item remained on the computer screen until the subject entered an 'Old' or 'New' judgment (left or right button push). 'Old' responses indicated that they thought the word was on the previous study list while 'New' responses indicated that they did not. Following this response, a '?' appeared on the screen. For items endorsed as 'Old' the subject had to then make a 'Remember' or 'Know' judgment (top or bottom button push). When the word was thought 'New', subjects were asked to simply press the same button again to advance to the next item.

For the short-delay condition, set-up for ERP recording was completed immediately after the study phase (this time largely involved reducing the impedances of the scalp electrodes and giving test instructions). The average delay from study to test in this group was 39 min (range: 27 to 56 min). For the long-delay condition, the elastic cap and electrodes were removed after the study session and the subject was scheduled to come back the next day. After ERP set-up was complete and the instructions delivered, the test phase began. The average delay between study and test for the long-delay group was 23 h, 34 min (range: 17 h, 45 min to 25 h, 20 min).

4.4. *Electrophysiological recording*

ERPs were recorded from 35 active tin electrodes that were held in place on the scalp by an electrode cap (Electro-Cap International, Eaton, OH, USA). Electrode locations were based on the International 10–20 system and were arranged in 5 columns, each with 7 antero-posterior sites. The midline sites were FPz, Fz, FCz, Cz, CPz, Pz, and Oz. There were two inner lateral columns that included FP1/2, F3/4, FC3/4, C3/4, CP3/4, P3/4, O1/2 and two outer lateral columns that included AF7/8, F7/8, FT7/8, T7/8, TP7/8, P7/8, PO7/8. All sites were referenced to the left mastoid. An electrode was placed below the left eye (LE) for detection of eye blinks and vertical eye movements (electrical activity at LE was compared to an electrode above the eye to monitor for these eye movements). Another electrode was placed at the right lateral canthus (referenced to an electrode at the left lateral canthus) to detect horizontal eye movements. The EEG was amplified (0.01 to 40 Hz, SAI BioAmplifier system), and the recorded data were continuously digitized (200 Hz) beginning 100 ms before onset of the test word.

4.5. *ERP analysis*

Continuous EEG data were divided off-line into epochs beginning 100 ms prior to test item presentation and ending 1170 ms after test item presentation. Trials with amplifier blocking or eye movements were excluded; blinks were corrected (Dale, 1994). Only ERPs formed from 16 or more artifact free trials were accepted for analysis to provide adequate signal-to-noise (Wilding and Rugg, 1997b). Separate ERPs were calculated for the following response types: 1) 'Remember' (studied items given an 'Old' and 'Remember' response; mean trials: 142.2, SD: 50.4), 2) 'Know' (studied items given an 'Old' and 'Know' response; mean trials: 87.8, SD: 30.8), 3) correct rejections (non-studied items given a 'New' response; mean trials: 178.9, SD: 54.8), and 4) false alarms (non-studied items given an 'Old' response; mean trials: 105.2, SD: 52.4). Mean amplitude (relative to a 100 ms pre-stimulus baseline) was calculated for each response type at each electrode for evaluation of the FN400 (300–500 ms), LPC (500–800 ms), and late frontal effect (800–1170 ms). These intervals were chosen based upon the ERP recognition memory literature (Curran, 2004; Curran and Cleary, 2003; Finnigan et al., 2002; Nessler et al., 2001; Rugg et al., 1998a) and visual inspection of the current data. While the FN400 and LPC intervals used here have been similarly examined in a number of studies, intervals for the late frontal effect have varied significantly to capture this effect [e.g., 1000–1500 ms (Curran, 2004); 800–1800 ms (Curran and Friedman, 2003); 800–1100 ms and 1100–1400 ms (Rugg et al., 2000; Wilding and Rugg, 1997a); 500–1400 ms (Wilding and Rugg, 1997b); 800–1200 ms, 1200–1600 ms, and 1600–1944 ms (Allan and Rugg, 1998); 600–900 ms, 900–1400 ms, and 1400–1900 ms (Donaldson and Rugg, 1999); 830–1450 ms (Trott et al., 1999); 1300–1900 ms (Duzel et al., 1997)]. Given this heterogeneity and in this context, the current interval was chosen to best isolate the observed frontal effect after the offset of the LPC and through to the end of the recording epoch. In cases of electrode failure, voltages were calculated as the average of two contiguous electrodes (this occurred at one electrode in five subjects, two in one subject, and three in one subject).

In general, the intervals of interest were analyzed using analysis of variance (ANOVA), with delay (short-delay, long-delay) as the between-subjects variable and response type, anterior–posterior (a–p; prefrontal, frontal, central, parietal, occipital), and laterality (left outer lateral, left inner lateral, midline, right inner lateral, right outer lateral) as the within-subjects variables. The electrode sites making up these columns and anterior–posterior rows can be seen in Fig. 1. This broad-distribution of electrodes was used to analyze the data in order to incorporate the full extent of ERP effects apparent by visual inspection for the intervals of interest. The Greenhouse–Geisser correction procedure was used for repeated measures factors with greater than one numerator degree of freedom. Effect size (η^2) of main effects of response type and interactions with delay group are reported. Additionally, interactions with delay were further analyzed separately for each group to better understand such interactions. Main effects of location (either laterality or a–p) and non-significant interactions are not reported unless of theoretical significance. Planned comparisons at specific electrode locations were carried out based on the literature. All P values reported are 2-tailed and were considered significant if they were less than 0.05.

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