On the sensitivity of event-related fields to recollection and familiarity

Short Title: ERFs, Recollection and Familiarity

Lisa H. Evans[1] and Edward L. Wilding[2]*

1. Cardiff University Brain Research Imaging Centre (CUBRIC), School of Psychology, Cardiff University, Cardiff, United Kingdom
2. School of Psychology, Nottingham University, Nottingham, United Kingdom

* Corresponding Author: edward.wilding@nottingham.ac.uk: Orcid ID: 0000-0002-9495-1418

Declarations of Interest: None

Abstract

The sensitivity of event-related potentials (ERPs) to the processes of recollection and familiarity has been explored extensively, and ERPs have been used subsequently to infer the contributions these processes make to memory judgments under a range of different circumstances. It has also been shown that event-related fields (ERFs, the magnetic counter-parts of ERPs) are sensitive to memory retrieval processes. The links between ERFs, recollection and familiarity are, however, established only weakly. In this experiment, the sensitivity of ERFs to these processes was investigated in a paradigm used previously with ERPs. An early frontally distributed modulation varied with memory confidence in a way that aligns it with the process of familiarity, while a later parietally distributed modulation tracked subjective claims of recollection in a way that aligns it with this process. These data points strengthen the argument for employing ERFs to assess the contributions these processes can make to memory judgments, as well as for investigating the nature of the processes themselves.

Keywords: Recollection, Familiarity, MEG, Confidence, Remember-Know, ERPs.

1. Introduction

Memories for experiences are widely considered to receive contributions from two processes (Mandler, 1980, 1991; Wixted & Mickes, 2010; A.P. Yonelinas, 2002). Recollection is recovery of qualitative information about an event. Familiarity is a scalar strength signal that can support certain kinds of memory judgments. The evidence for the distinction between these processes spans behavioural, neuropsychological, and functional brain imaging research in humans, alongside studies in other animals (Aggleton & Brown, 1999; Aggleton et al., 2005; Rugg & Curran, 2007; Vargha-Khadem et al., 1997; Yonelinas, Otten, Shaw, & Rugg, 2005).

Event-related potentials (ERPs) have been employed widely in studies designed to test claims about the validity of the separation between the processes of recollection and familiarity (Allan, Wilding, & Rugg, 1998; Friedman & Johnson, 2000; Wilding & Ranganath, 2012). In other studies, ERPs have been employed alongside behavioural data to adjudicate between accounts of how one or both of these processes support memory characteristics such as source (context) judgments (Diana, Van den Boom, Yonelinas, & Ranganath, 2011), judgments of recency (Grove & Wilding, 2009), testing effects (Bai, Bridger, Zimmer, & Mecklinger, 2015), and the revelation effect (Azimian-Faridani & Wilding, 2004).

The use of ERPs in these ways was preceded by studies in which the sensitivity of ERP old/new effects to the processes of recollection and familiarity was investigated (for review, see Wilding & Ranganath, 2012). Old/new effects are differences between neural activities for old (studied) and new (unstudied) test items attracting correct old/new judgments. The left-parietal old/new effect is prominent between 500 and 800 ms post-stimulus over left-posterior-parietal scalp, and has been linked with the process of recollection (Allan et al., 1998). The mid-frontal old/new effect has a fronto-central scalp maximum between 300 and 500 ms post-stimulus and has been linked with the process of familiarity (for key data and discussion of alternative accounts, see Bridger, 2012; Paller, Voss, & Boehm, 2007; Rugg & Curran, 2007).

Somewhat less attention has been paid to event-related fields (ERFs), and far fewer studies have been designed to test the sensitivity of ERFs to recollection and familiarity. That is the intention of the research described here. This builds on indications of the general sensitivity of MEG measures to memory processes, which has been accomplished via assessment of ERFs (Tendolkar et al., 2000; Walla et al., 1999; Walla, Hufnagl, Lindinger, Deecke, Imhof, et al., 2001; Walla, Hufnagl, Lindinger, Deecke, & Lang, 2001), time-frequency plots (Düzel, Habib, Guderian, & Heinze, 2004; Düzel et al., 2003; Guderian & Düzel, 2005; Neufang, Heinze, & Düzel, 2006), and/or data transformed into source space (Dhond, Witzel, Dale, & Halgren, 2005; Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Lee, Simos, Sawrie, Martin, & Knowlton, 2005; Seibert, Hagler, & Brewer, 2011).

For ERFs, Düzel and colleagues (Düzel, Neufang, & Heinze, 2005) identified three temporally and spatially separable ERF modulations comprising changes in signal strength for items that attracted correct 'old' rather than correct 'new' judgments. One of these old/new effects was most prominent over left-posterior scalp from 500 to 800ms post-stimulus (see also Tendolkar et al., 2000), while another was prominent over left-frontal scalp between 300 and 500ms. The third was largest over occipito-temporal scalp locations between 250 and 350ms. What are likely to be the same three modulations were identified in a later study (Bridson, Muthukumaraswamy, Singh, & Wilding, 2009) and in their experiment the three were shown to be functionally dissociable.

In each of these studies, however, the task manipulations did not permit a strong basis for separating responses associated with familiarity or recollection. This limitation does not apply to the study reported by Staresina and colleagues (2005), however, who asked participants to make old/new judgments and then, for old judgments, a binary (high/low) confidence judgment. They reasoned that highly confident judgments are based upon a relatively greater contribution from recollection than from familiarity. They did not, however, observe any ERF modulations that varied with response confidence.

Bergstrom and colleagues (Bergström, Henson, Taylor, & Simons, 2013) also examined the sensitivity of ERFs to recollection, although the baseline condition in their study (a semantic retrieval requirement) makes comparison of their data to others difficult. Horner and colleagues (2012) acquired MEG data in a task where participants made old/new judgments and then context judgments. Confidence in the context judgment was also assessed. They reported old/new effects over occipito-temporal and left-frontal scalp with the same temporal characteristics as those described by Düzel et al. and by Bridson and colleagues (Bridson et al., 2009; Düzel et al., 2005). While these modulations were not sensitive to the accuracy of context judgments, there was some evidence that a later modulation (500 to 600ms), also with a left-frontal maximum, was sensitive to the accuracy of context judgments. This outcome would align this activity with the process of recollection, rather than familiarity.

In the study that is most relevant to the one described here, Evans and Wilding (2012) measured neural activity while people were exposed to new and old words. They employed the Remember/Know paradigm, in which, upon encountering an item they believe they have studied previously, participants must make either a Remember or a Know response. The former is to be given when specific details about the previous encounter can be recovered, and the latter when only a feeling a familiarity drives the view that an item was encountered previously (Rajaram, 1993; Tulving, 1985).

In keeping with the logic detailed in many places, Evans and Wilding (2012) noted that, if there is neural activity signalling the process of recollection, then it should be evident to a greater degree when people make a Remember rather than a Know response, assuming that a Remember response is based primarily on recollection (Rajaram, 1993; Smith, 1993; Tulving, 1985). A modulation with a left-parietal maximum peaking between 500 and 800 ms post-stimulus behaved in this way, mirroring previous findings with ERPs (Paller & Kutas, 1992).

Evans and Wilding also observed a modulation in the 300-500 ms post-stimulus window at frontal sites that was larger for Know than for Remember responses. They linked this modulation with the process of familiarity, because under certain circumstances a neural index of familiarity should behave in this way (for similar arguments, see Berry et al, 2012; Yu et al, 2010). While the spatial distribution and time-course of the modulation they reported is consistent with that of the mid-frontal ERP old/new effect, for ERPs there has been little evidence for larger early memory effects for Know rather than Remember judgments (Smith, 1993). This is also true for memoranda attracting correct or incorrect source judgments, which in some ways parallels the Remember/Know separation (Senkfor & Van Petten, 1998; Trott, Friedman, Ritter, & Fabiani, 1997; Wilding & Rugg, 1996). We return to the issue of differential sensitivity of ERPs and ERFs to the same process in the Discussion.

In summary, there is some evidence for the sensitivity of ERFs to the processes of recollection and familiarity, and arguably a stronger case for the former than the latter. The experiment reported here was designed to test further the functional significance of the ERFs that have been linked to recollection and familiarity. The behavioural process separation was accomplished by employing a variant of the Remember/Know paradigm that has been used previously in functional imaging studies (Woodruff, Hayama, & Rugg, 2006; Yonelinas et al., 2005; Yu et al., 2010).

In an initial study phase participants were exposed to a list of words. In a subsequent test phase participants saw studied and unstudied words that were shown one at a time. Participants were asked to give a Remember response for words where they could recover details of the study encounter. For all other test words they were asked to make old/new judgments on a four-point confidence scale (confident/unconfident Know; confident/unconfident New).

Following the logic of earlier studies (Woodruff et al., 2006; Yonelinas et al., 2005), if the early anterior modulation described above indexes familiarity, then it will vary with response confidence, differentiating in a graded manner the confidence categories in the following order: confident Know, unconfident Know, unconfident New, confident New. If the later modulation indexes recollection, then it will be reliable only for words attracting Remember responses.

2. **Method**

2.1. Participants

These were 35 right-handed, healthy native English speakers. All gave informed consent and the experiment was approved by the Cardiff University School of Psychology Ethics Committee. The analyses reported here are from 20 participants (17 females; age range: 18-26). Fifteen participants were excluded; 8 because they failed to contribute sufficient trials (>14) to one or more of the critical experimental conditions after artefact rejection; 6 participants because of artefacts in the MEG signal (of these 2 were due to metal interference, 2 for excessive alpha activity and 2 due to large ocular artefacts); and 1 participant because of poor discrimination (a hit minus false alarm score < 0.2: the values for hits and false alarms were calculated by summing the probabilities of Remember, Confident and Unconfident old responses to old and new words, respectively). The averaged behavioural outcomes for all 35 participants are shown in Appendix 1.

2.2. Stimuli

A pool of 450 words (all concrete nouns) was used. Words were 3-13 letters long (mean = 6.3) and had a mean written frequency of 18.8 counts/million and range of 10-30 (Kucera & Francis, 1967). Five lists of 75 words were constructed by selecting words randomly from the pool. Each participant received three of these lists at study. The remaining two lists were designated as new words and were intermixed randomly with the study items to form the test list. Five complete experiment lists were created such that each word was encountered at study and at test in three versions, and at test only in two versions. An additional 75 words were employed for practice phases (50 of these for the practice study list, all 75 for the test list).

2.3. Procedure

Once participants had given informed consent and were situated below the MEG dewar, they completed a practice session. They were seated 2m from a monitor on which all stimuli were presented in white on a black background at fixation (subtending maximum visual angles of 0.2° vertically and 2.3° horizontally). For the test phase of the practice session participants were asked to justify their responses on each trial verbally.

There was one study block with 225 trials. Participants had a short break after every 75 trials. Each trial started with presentation of a fixation cross for 1000ms, the study word (300ms) and then a blank screen. Participants were asked to judge whether each word referred to an animate or inanimate object, responding via keypress with their left and right index fingers, respectively. 1000ms after a response was made a screen displaying the instruction "BLINK NOW" was shown for 1000ms. Trials where no response was registered within 5000ms of stimulus offset were treated as errors and the next trial started automatically.

There was a 10min break between study and test phases. Participants were able to get up and walk around before being seated back beneath the dewar. The instructions for the test phase were reiterated before the test phase began. There was a single test block (375 trials) and participants were given a break every 75 trials. The structure and timing of study and test trials was identical: all that differed were the response requirements. Participants were asked for a five-way judgement to each test word. They were asked to give a Remember response if they believed the word had been shown at study and in addition if any detail from study could be recalled (Rajaram, 1993; Rajaram & Roediger, 1997). This response was made via a button press with the thumb. Participants were instructed that, if no contextual information could be retrieved the test words were to be judged on a 4-point confidence scale with button presses using the other hand: confident Know (thumb), unconfident Know (index finger), unconfident New (middle finger) and confident New (ring finger). Participants were instructed that a Know response should reflect their view that the test word had been shown at study, albeit in the absence of memory for specific contextual information. A New response reflected the view that the test word had not been shown at study.

The hands participants responded with at study and at test were counterbalanced, but the mapping of responses to digits was retained. In both phases participants were asked to be as accurate and as quick as possible. They were also asked to keep their head as still as possible throughout the experiment and to keep their eyes focussed on the centre of the screen. They were asked to try to blink only when the "BLINK NOW" message was visible on-screen.

2.4. MEG recording, processing and analysis

MEG was recorded during study and test phases. Test data only are presented here. Whole-head recordings were taken using a 275-channel CTF radial gradiometer system. The sampling rate was 300Hz. An additional 29 reference channels were recorded for noise cancellation purposes, and the primary sensors were analysed as synthetic third-order gradiometers (Vrba & Robinson, 2001). Four of the 275 channels were turned off due to excessive sensor noise. Participants were seated upright in a dimmed magnetically shielded room. Data were acquired continuously, then epoched offline into 2100ms segments including a 100ms baseline relative to which all mean signal strengths were measured. Trials containing large signal and/or EOG artefacts were excluded prior to averaging, based on visual inspection of data for each participant, blind to condition at the time of pre-processing. Average ERFs were formed for each participant for Remember, confident Know and unconfident Know responses to old words and also to unconfident New and confident New responses to new words. The mean numbers of trials in each response category were as follows: Remember = 70 (range 16-142), confident Know = 56 (16-120), unconfident Know = 30 (14-72), unconfident new = 40 (16-78), confident new = 52 (16-102).

To test the proposal that ERFs index familiarity (Bridson et al., 2009; Evans, 2012), signal strengths associated with the critical response categories were analysed for data for the 300-500ms post-stimulus time period taken from a cluster of sensors over anterior scalp locations. Further analyses were conducted on data taken from the 500-800ms period from a cluster of sensors over posterior-parietal scalp, where activity linked with the process of recollection has been identified previously (Bridson et al., 2009; Evans & Wilding, 2012).

To identify the specific sensors at which activities linked to these processes were largest in these time windows a full-width half maximum (FWHM) approach was adopted, recognising that variation in head-shape and orientation in the dewar will result in small differences between the maxima of effects of interest across ostensibly similar studies. In this procedure the sensor with the maximum value was found in each time window (300-500 and 500-800ms). Those sensors that exceeded half the value of the peak sensor were included in the cluster.

The FWHM computation was completed over difference scores that were calculated to reflect activity differentiating between correct responses to old and new items in a way that is not biased towards responses that might be based on recollection or familiarity. This was accomplished by subtracting signal strength estimates for correct rejections from those for hits. Correct rejection estimates were obtained for each participant via an average of signal strengths for confident and unconfident New responses given to new test words. The hit strength estimates for each participant was derived in two stages. First, by calculating the average of confident and unconfident Know responses to old test words. Second, by computing an unweighted average of this estimate and that obtained from Remember responses to old words.

3. **Results**

3.1. Behaviour

The proportions of old and new words attracting each of the five response options are shown in Table 1. For old words, Remember responses dominate, with the proportions dropping from correct through to incorrect old judgments. The opposite pattern can be seen for the distribution of responses to new words, and this cross-over is reflected in a reliable interaction obtained in a 2*5 ANOVA with factors of word status and response option ($F(2.76,52.46) = 76.70$, $p<.001$). In this and in all subsequent ANOVAs the Geisser-Greenhouse correction (Winer, 1971) was employed as appropriate and epsilon-corrected degrees of freedom are shown in the text.

Also displayed in Table 1 are the reaction times (RTs) for each response category. These are collapsed across study status. A one-way ANOVA with five levels revealed a main effect of response category ($F(2.37, 45.06) = 29.41$, $p<.001$), because responses are quickest for high confidence New and for Remember responses.

3.2.Event-Related Fields (ERFs)

Figure 1 shows the scalp distributions of the neural activities averaged over the 300-500 and 500-800ms time periods that differentiate correct responses to old and new test words. The maps were computed from difference scores obtained by subtracting mean signal strengths associated with correct rejections from the unweighted average of Remember and Know responses to old items (see section 2.4.). The FWHM procedure based on these data resulted in the identification of a cluster of 11 sensors over left-frontal scalp in the 300-500ms epoch[1] The largest difference (27 fT) was at sensor LT22. For the 500-800ms epoch the largest difference was at sensor LT27 (28 fT) and the FWHM procedure resulted in a cluster comprising 17 sensors over left occipito-temporal scalp[2]. Both of these cluster locations resemble closely those identified in previous MEG studies by Evans, Wilding and colleagues (Bridson et al., 2009; Evans & Wilding, 2012).

3.2.1.300-500ms

Figure 2 (a) shows representative ERFs for the critical response categories from sensors located over left-frontal scalp. The panel below the ERFs displays the mean signal strengths for the five key response categories. An initial analysis established that, when collapsed across response confidence, mean signal strength for Know responses was reliably greater than that for Correct Rejections ($t(19) = 2.44$, $p = .025$).

The critical question is how the signal strengths vary for the four categories associated with explicit confidence judgments: a graded change as described in the Introduction would favour a familiarity account for this modulation (Woodruff et al., 2006; Yonelinas et al., 2005; Yu et al., 2010). To assess this possibility an analysis strategy was adopted that has been employed previously in similar fMRI (Yonelinas et al., 2005) and ERP studies (Woodruff et al., 2006; Yu et al., 2010). For each participant a regression coefficient was calculated using the mean signal from the cluster in the 300-500ms window along with a dummy variable reflecting the four confidence levels. If the null hypothesis (no relationship between ERF magnitudes and confidence) is correct then across participants the mean of the beta coefficients will approximate zero. Contrary to the null hypothesis, the coefficients differed significantly from zero ($t(19) = 2.90$, $p <.01$).

As noted in the Introduction, Evans and Wilding (2012) reported that signal strength at similar scalp locations was greater for old words attracting Know rather than Remember responses. This difference (-75vs -76 fT), did not reach significance here ($t(19) <1$), while the old/new effect for Remember responses was reliable ($t(19) = 2.90$, $p < .01$)

3.2.2.500-800ms

Evans and Wilding (2012) also reported that at posterior-parietal sites old words attracting Remember responses were associated with reliably greater signal strength than old words attracting Know responses, as well as correctly rejected new words. The relevant data and ERFs for all five key response categories are shown in Figure 2(b). Three planned paired analyses based on their outcomes were conducted and revealed the same two reliable outcomes they reported (2012): While Know responses were not reliably different from Correct Rejections, Remember responses were associated with greater signal strength than both of these response categories (collapsed across confidence: R vs CR: $t(19) = 3.72$, $p < .01$; R vs K: $t(19) = 2.41$, $p < .05$).

While these outcomes replicate those in our earlier study, the pattern of data in Figure 2 suggests a graded response to old items. Post-hoc t-tests (adjusted alpha = .0125) did not, however, reveal reliable old/new effects for correct confident or unconfident Know judgments (relative to the confident New baseline), reliable differences between Remember and confident Know judgments to old words, nor between new words attracting confident or unconfident judgments.

4. Discussion

This experiment was designed to assess the functional significance of ERF modulations that might index the processes of familiarity and recollection. A link between an early anteriorly distributed modulation and familiarity was first suggested by Bridson and colleagues (2009). This suggestion was based primarily on the temporal and spatial similarities between this modulation and the mid-frontal ERP old/new effect, for which several authors have suggested a link with the process of familiarity (for a review, see Rugg & Curran, 2007).

This functional account was adopted by Evans and Wilding (2012). They used ERFs to argue for a model of independence between the processes of familiarity and recollection, based around how this early ERF modulation behaved in a Remember/Know task. The experiment reported here was designed to test this assumption, as well as to assess the (arguably more established) link between a parietally distributed ERF old/new effect and the process of recollection (Allan et al., 1998).

Temporally and spatially similar modulations to those observed by Evans and Wilding (2012) were obtained here. Turning first to putative indices of familiarity, activity at a cluster of electrodes over left-frontal scalp from 300-500ms tracked familiarity strength, in so far as confidence in old/new status is a proxy for strength. Figure 2 shows a linear relationship between confidence and mean signal strengths, and this was corroborated in the analyses reported above.

Comparable data patterns have been reported previously for studies in which ERPs were employed, albeit with slightly different contrasts (Woodruff et al., 2006; Yu et al., 2010). In both of these experiments a contrast between ERPs for the four levels of confidence used here was reported. The contrasts were conducted over data collapsed across the old/new status of the test words. While the same graded pattern reported here was observed, in both cases additional analyses were reported. These were introduced in order to address the concern that the pattern arose simply because ERP amplitudes varied for old and new items, and the proportion of old items in each response category increased moving from ‘confident New’ through to ‘confident Old’.

Woodruff and colleagues (Woodruff et al., 2006) conducted an analysis where they selected trials to enable a contrast between categories associated with the same number of old and new items, and the same average confidence reported data. They argued that their null result in this analysis suggested that the graded pattern indicated that it was not the old/new status of items that drove the graded effect they observed in their primary analysis. Rather than relying on a null outcome, Yu et al. (2010) showed that a comparable graded pattern was found when averaged ERPs were restricted to old items and separated for three response categories: ‘confident Old’, ‘unconfident Old’ and ‘unconfident New’.

This analysis could not be conducted in this experiment because of the proportion of ‘unconfident New’ responses given to old words, and so we adopted a different approach. The confidence contrast was restricted to items attracting correct responses. The evidence that this modulation is not simply a reflection of greater signal strength for old than for new words is the graded function we have documented. If the modulation of interest simply reflected signal strength in this way than a step function would have been observed: greater signal strength for old words alongside no changes in signal according to confidence (separately) for old and for new words.

These data can therefore be interpreted as favouring a familiarity account of this ERF modulation. Other accounts of the functional significance of this modulation remain viable, however, and these are motivated by different accounts of the functional significance of the mid-frontal event-related potential (ERP) old/new effect. Paller and colleagues (Paller et al., 2007). have argued that many data points that have formed the basis for the familiarity account of this ERP old/new effect can equally well be accounted by an account in terms of processes supporting a facilitation in response times as a function of repetition of semantically related material.

For ERPs, the data that can adjudicate between these accounts have been discussed in several places (Bridger, 2012; Paller et al., 2007; Voss, Lucas, & Paller, 2012; Wilding & Evans, 2012). For ERFs, however, the limited data available can be accommodated equally well by a familiarity account and by a conceptual priming account, if it is assumed that the level of conceptual priming will co-vary with familiarity strength. What this means is that while it is possible to deploy this anterior ERF modulation to make functional claims about familiarity when the stimuli have conceptual content, it would be premature to extend the use of this modulation to stimulus sets where this semantic relationship does not hold.

Also of note is that the index linked to familiarity here did not behave in exactly the same way as in our earlier study (Evans & Wilding, 2012). In this experiment the modulation associated with Remember and with Know responses was indistinguishable. In our previous study it was larger for the latter, with that finding being critical for the argument that the processes of recollection and familiarity are independent (Evans & Wilding, 2012).

In keeping with the logic already outlined, Evans & Wilding (2012) noted that, if there is neural activity signalling the process of recollection, then it should be evident to a greater degree when people make a Remember rather than a Know response. They also observed that, if familiarity and recollection are independent, and if familiarity is a continuous strength signal, then all items given a Remember response will have a level of familiarity associated with them. For only a subset of these items, however, will the level of familiarity exceed the threshold sufficient to license a Know response. This contrasts with the levels of familiarity associated with Know responses, which by definition must exceed criterion in each instance. Over the course of a task in which many Remember and Know responses are given, therefore, the mean level of familiarity will be greater for items attracting Know rather than Remember responses.

It also follows from this argument that the size of the difference between a neural index of familiarity for items attracting Remember and Know responses will diminish as the overall likelihood of familiarity contributing to judgments goes up. Based on the recommendations for computing familiarity from Remember/Know data under an independence assumption (Yonelinas & Jacoby, 1995) estimates of familiarity were calculated. For this study the mean value is 0.74, whereas it was 0.50 in our previous study[3]. These outcomes therefore offer an explanation for the lack of correspondence across studies in the R/K data taken from anterior sensors in the 300—500ms time window.

Also of note is that the ERF modulation has, in two cases, showed what may be a greater sensitivity to changes in familiarity than its likely ERP counterpart. First, and as noted in the

Introduction, the ERF but not the ERP modulation separated studied words presented twice from those presented only once at test (Bridson et al., 2009). Second, indications of larger mid-frontal ERP old/new effects for Know than for Remember responses have not been obtained (Smith, 1993). These outcomes raise the possibility that the ERF index presents some advantages if the question of interest depends upon changes in a neural index of familiarity.

Turning to the 500-800ms epoch, there are some correspondences between the outcomes and those reported previously by Evans & Wilding (2012). In keeping with the earlier findings, an old/new effect was reliable only for Remember responses, and was reliably larger than the effect for Know responses. In terms of statistical outcomes, therefore, the data in the two studies correspond closely. Figure 2, however, shows that ERF signal strengths for confident and unconfident Know responses lie between those for Remember responses and for correct rejections, and are numerically greater for high than for low confidence Know responses. Post-hoc tests for ERFs separated by confidence did not reveal reliable differences between old items attracting correct responses, but the same was also true for new items.

How should these trends be considered? The absence of differences (both statistically and numerically) between new items attracting confident or unconfident new judgments, and indeed the absence of a larger modulation for confident new than unconfident old responses, argues against an interpretation solely in terms of response confidence, as well as any interpretation of the data in terms of familiarity strength. The apparently graded pattern for old words (Remember > confident Know > unconfident Know) remains a challenge, however.

The temporal and spatial correspondence between this modulation and that observed in comparable ERP studies suggests a link between this modulation and the process of recollection. In light of this, the trends in Figure 2 (albeit not supported by statistical outcomes) can be accommodated by assuming that a Remember response is given only when a certain level or quality of content is recovered. In this sense the data are consistent with the view that recollection is graded (Elfman, Aly, & Yonelinas, 2014). This explanation does not sit as well, however, with the absence of a comparable modulation associated with Know responses in our earlier study (2012).

Two differences between the designs of the two experiments merit consideration. The first is the use of confidence ratings in this experiment only: It is possible that the confidence manipulation influenced the way in which participants decided whether items should attract a Remember or a Know response. The second difference is the encoding tasks for the critical retrieval contrasts: shallow encoding in the earlier study (Evans & Wilding, 2012), deep encoding in this study. It is possible that the criteria for producing a Know response vary with encoding context, and resolving the apparent differences across the findings in these studies is important for delineating in detail the functional properties of recollection.

4.1. Summary. This experiment was conducted to assess the sensitivity of ERFs to the processes of familiarity and recollection. The design was a close variant of one employed previously to identify neural activity linked with familiarity in fMRI (Yonelinas et al., 2005) and ERP (Woodruff et al., 2006; Yu et al., 2010) studies of memory retrieval. The graded manner in which ERPs at anterior locations from 300 to 500ms tracked response confidence and item status is consistent with the view that this MEG signal can act as an index of familiarity, at least for stimuli with conceptual content. While the statistical outcomes for the data from 500-800ms at posterior occipital sensors match those obtained previously (Evans & Wilding, 2012), and are consistent with the view that this effect is a neural index of recollection, the trends in the data for Know responses were unexpected. They indicate that further examination of ERFs, and possibly ERPs, has the potential to contribute to the debate over the properties of this fundamental retrieval process.

Footnotes:

1. The sensors in the early time window at left frontal scalp were: LF46, LF56, LT11, LT12, LT13, LT21, LT22, LT23, LT33, LT41, LT42.
2. The sensors in the later time window at left parietal scalp were: LT16, LT26, LT27, LT37, LO12, LO13, LO14, LO22, LO23, LO24, LO31, LO32, LO33, LO34, LO42, LO43, LO44.
3. These calculations are based on the behavioural data taken from the shallow encoding condition reported by Evans & Wilding (2012). The data from this condition contributed the critical ERP data upon which claims regarding a relationship of independence between the processes of recollection and familiarity were made.

References:

Aggleton, J. P., & Brown, M. W. (1999). Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behavioural and Brain Sciences, 22*, 425-489.

Aggleton, J. P., Vann, S. D., Denby, C., Dix, S., Mayes, A. R., Roberts, N., et al. (2005). Sparing of the familiarity component of recognition memory in a patient with hippocampal pathology. *Neuropsychologia, 43*, 1810-1823.

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

Azimian-Faridani, N., & Wilding, E. L. (2004). An event-related potential study of the revelation effect. *Psychonomic Bulletin and Review, 11*, 926-931.

Bai, C.-H., Bridger, E., Zimmer, H., & Mecklinger, A. (2015). The beneficial effect of testing: an event-related potential study. *Frontiers in Behavioral Neuroscience, 9*(248).

Bergström, Z. M., Henson, R. N., Taylor, J. R., & Simons, J. S. (2013). Multimodal imaging reveals the spatiotemporal dynamics of recollection. *NeuroImage, 68*, 141-153.

Berry, C. J., Shanks, D.R., Speekenbrink, M., Henson, R.N.A. (2012). Models of recognition, repetition priming, and fluency: exploring a new framework. *Psychological Review, 119*, 40-79.

Bridger, E. K., Bader, R., Kriukova, O., Unger, K., Mecklinger, A. (2012). The FN400 is functionally distinct from the N400. *Neuroimage, 63*, 1334-1342.

Bridson, N. C., Muthukumaraswamy, S., Singh, K. D., & Wilding, E. L. (2009). Magnetoencephalographic correlates of processes supporting long-term memory judgments. *Brain Research, 1283*, 73-83.

Dhond, R. P., Witzel, T., Dale, A. M., & Halgren, E. (2005). Spatiotemporal brain maps of delayed word repetition and recognition. *NeuroImage, 28*, 293-304.

Diana, R. A., Van den Boom, W., Yonelinas, A. P., & Ranganath, C. (2011). ERP correlates of source memory: Unitized source information increases familiarity-based retrieval. *Brain Research, 1367*, 278-286.

Düzel, E., Habib, R., Guderian, S., & Heinze, H. J. (2004). Four types of novelty-familiarity responses in associative recognition memory of humans. *European Journal of Neuroscience, 19*, 1408-1416.

Düzel, E., Habib, R., Schott, B., Schoenfeld, A., Lobaugh, N., McIntosh, A. R., et al. (2003). A multivariate, spatiotemporal analysis of electromagnetic time-frequency data of recognition memory. *NeuroImage, 18*, 185-197.

Düzel, E., Neufang, M., & Heinze, H. J. (2005). The oscillatory dynamics of recognition memory and its relationship to event-related responses. *Cerebral Cortex, 15*, 1992-2002.

Elfman, K. W., Aly, M., & Yonelinas, A. P. (2014). Neurocomputational account of memory and perception: Thresholded and graded signals in the hippocampus. *Hippocampus, 24*, 1672-1686.

Evans, L. H., Wilding, E.L. (2012). Recollection and familiarity make independent contributions to recognition memory. *Journal of Neuroscience, 32*, 7253-7257.

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

Gonsalves, B. D., Kahn, I., Curran, T., Norman, K. A., & Wagner, A. D. (2005). Memory strength and repetition suppression: multimodal imaging of medial temporal cortical contributions to recognition. *Neuron, 47*, 751-761.

Grove, K. L., & Wilding, E. L. (2009). Retrieval processes supporting judgments of recency. *Journal of Cognitive Neuroscience, 21*, 461-473.

Guderian, S., & Düzel, E. (2005). Induced theta oscillations mediate large-scale synchrony with mediotemporal areas during recollection in humans. *Hippocampus, 15*, 901-912.

Horner, Aidan J., Gadian, David G., Fuentemilla, L., Jentschke, S., Vargha-Khadem, F., & Duzel, E. (2012). A Rapid, Hippocampus-Dependent, Item-Memory Signal that Initiates Context Memory in Humans. *Current Biology, 22*, 2369-2374.

Kucera, H., & Francis, W. N. (1967). *Computational analysis of present-day American English*. Providence, RI: Brown University Press.

Lee, D., Simos, P., Sawrie, S. M., Martin, R. C., & Knowlton, R. C. (2005). Dynamic brain activation patterns for face recognition: A magnetoencephalography study. *Brain Topography, 18*, 19-26.

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

Mandler, G. (1991). Your face looks familiar but I can't remember your name: A review of dual process theory. In W. E. Hockley & S. Lewandowsky (Eds.), *Relating Theory and Data: Essays on Human Memory in Honor of Bennet B. Murdock* (pp. 207-225). Hillsdale, NJ: Erlbaum.

Neufang, M., Heinze, H. J., & Düzel, E. (2006). Electromagnetic correlates of recognition memory processes. *Clinical EEG and Neuroscience, 37*, 300-308.

Paller, K. A., & Kutas, M. (1992). Brain potentials during retrieval provide neurophysiological support for the distinction between conscious recollection and priming. *Journal of Cognitive Neuroscience., 4*, 375-391.

Paller, K. A., Voss, J. L., & Boehm, S. G. (2007). Validating neural correlates of familiarity. *Trends in Cognitive Sciences, 11*, 243-250.

Rajaram, S. (1993). Remembering and knowing: Two means of access to the personal past. *Memory and Cognition, 21*, 89-102.

Rajaram, S., & Roediger, H. L. I. (1997). Remembering and knowing as states of consciousness during retrieval. In J. D. Cohen & J. W. Schooler (Eds.), *Scientific approaches to consciousness* (pp. 213-240). Mahwah, NJ: Lawrence Erlbaum Associates.

Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences, 11*, 251-257.

Seibert, T. M., Hagler, D. J., & Brewer, J. B. (2011). Early parietal response in episodic retrieval revealed with MEG. *Human Brain Mapping, 32*, 171-181.

Senkfor, A. J., & Van Petten, C. (1998). Who said what: An event-related potential investigation of source and item memory. *Journal of Experimental Psychology: Learning, Memory and Cognition, 24*, 1005-1025.

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

Staresina, B. P., Bauer, H., Deecke, L., & Walla, P. (2005). Magnetoencephalographic correlates of different levels in subjective recognition memory. *Neuroimage, 27*, 83-94.

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

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

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

Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W., & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science, 277*, 376-380.

Voss, J. L., Lucas, H. D., & Paller, K. A. (2012). More than a feeling: Pervasive influences of memory without awareness of retrieval. *Cognitive Neuroscience, 3*, 193-207.

Vrba, J., & Robinson, S. E. (2001). Signal processing in magnetoencephalography. *Methods, 25*, 249-271.

Walla, P., Endl, W., Lindinger, G., Lalouschek, W., Deecke, L., & Lang, W. (1999). Early occipito-parietal activity in a word recognition task: an EEG and MEG study. *Clinical Neurophysiology, 110*, 1378-1387.

Walla, P., Hufnagl, B., Lindinger, G., Deecke, L., Imhof, H., & Lang, W. (2001). False recognition depends on depth of prior word processing: a magnetoencephalographic (MEG) study. *Cognitive Brain Research, 11*, 249-257.

Walla, P., Hufnagl, B., Lindinger, G., Deecke, L., & Lang, W. (2001). Physiological evidence of gender differences in word recognition: a magnetoencephalographic (MEG) study. *Cognitive Brain Research, 12*, 49-54.

Wilding, E. L., & Evans, L. H. (2012). Electrophysiological correlates of memory processes. *Cogn Neurosci, 3*, 217-218.

Wilding, E. L., & Ranganath, C. (2012). Electrophysiological correlates of episodic memory processes. In S. J. Luck & E. Kappenman (Eds.), *The Oxford Handbook of ERP Components* (pp. 373-396). Oxford: Oxford University Press.

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

Winer, B. J. (1971). *Statistical principles in experimental design.* New York: McGraw-Hill.

Wixted, J. T., & Mickes, L. (2010). A continuous dual-process model of remember/know judgments. *Psychological Review, 117*, 1025-1054.

Woodruff, C. C., Hayama, H. R., & Rugg, M. D. (2006). Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Brain Research, 1100*, 125-135.

Yonelinas, A. P. (2002). The nature of recollection and familiarity: a review of the 30 years of research. *Journal of Memory and Language, 46*, 441-517.

Yonelinas, A. P., & Jacoby, L. L. (1995). The relationship between remembering and knowing as bases for recognition: Effects of size congruency. *Journal of Memory and Language, 34*, 622-643.

Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *Journal of Neuroscience, 25*, 3002-3008.

Yu, S. S., Rugg, M.D. (2010). Dissociation of the electrophysiological correlates of familiarity strength and item repetition. *Brain Research, 1320*, 74-84.

Acknowledgments:

The authors would like to thank Suresh Muthukumaraswamy for technical support, and Amie Doidge, Jane Herron and Angharad Williams for comments on the manuscript. This research was funded by BBSRC grant number BB/I001247/1 awarded to both authors.

Figure Legends:

Figure 1. Scalp maps showing distributions of ERF activity for a) the 300-500ms, and b) the 500-800ms epochs. The maps were computed based upon a subtraction of correct rejections from the unweighted average of Remember and Know responses to old items, described in detail in the methods. The circles on each of the maps indicate the approximate location of the sensors selected via the FWHM procedure in each time window.

Figure 2. Averaged across participant event-related fields (ERFs) for the 5 critical response categories and averaged for the sensor clusters to which data from the 300-500ms (a: left-frontal) and 500-800ms (b: left posterior) epochs were analysed. The accompanying graphs for each location and epoch show mean signal strengths for the 5 key response categories for the same sensor clusters. R = Remember, CK = confident Know, UK = unconfident Know, UN = unconfident New, CN = confident New. Error bars = + 1 S.E.

Table 1. Proportions of old and new words assigned to each response category, with associated reaction times (collapsed across study status).

	Remember	Confident Know	Unconfident Know	Unconfident New	Confident New
Old	0.37	0.30	0.17	0.10	0.06
New	0.03	0.05	0.16	0.33	0.42
RT (ms)	1262	1591	1936	1799	1467

Appendix 1. Behavioural data for 35 participants.

Proportions of old and new words assigned to each response category, with associated reaction times (collapsed across study status).

	Remember	Confident Know	Unconfident Know	Unconfident New	Confident New
Old	0.39	0.26	0.17	0.11	0.06
New	0.04	0.06	0.18	0.34	0.38
RT (ms)	1230	1567	1813	1698	1433

Mirroring the statistical outcomes for the analyses for the 20 participants contributing sufficient trials to all 5 key response categories of interest, a 2*5 ANOVA of the accuracy data (factors of Old/New and Response) revealed a reliable interaction term: $F(3.09, 105.13) = 100.68$, $p<.001$). The data pattern is very similar overall to that shown for the 20 participants included in the main analyses (Table 1). As reported in Methods, 8 of the 15 participants excluded did not contribute sufficient trials to one of more of the key response categories to be included in the analyses. The correspondence between the numerical values in Table 1 and Appendix 1 reflects in part the fact that the specific categories for which there were insufficient trials varied across the excluded participants.

For the reaction time data, a one-way ANOVA with 5 levels revealed a main effect of response category ($F(2.46, 83.51) = 33.45$, $p<.001$), with this outcome reflecting the fact that the slowest responses are for low confidence responses (cf Table 1).

Figure 1

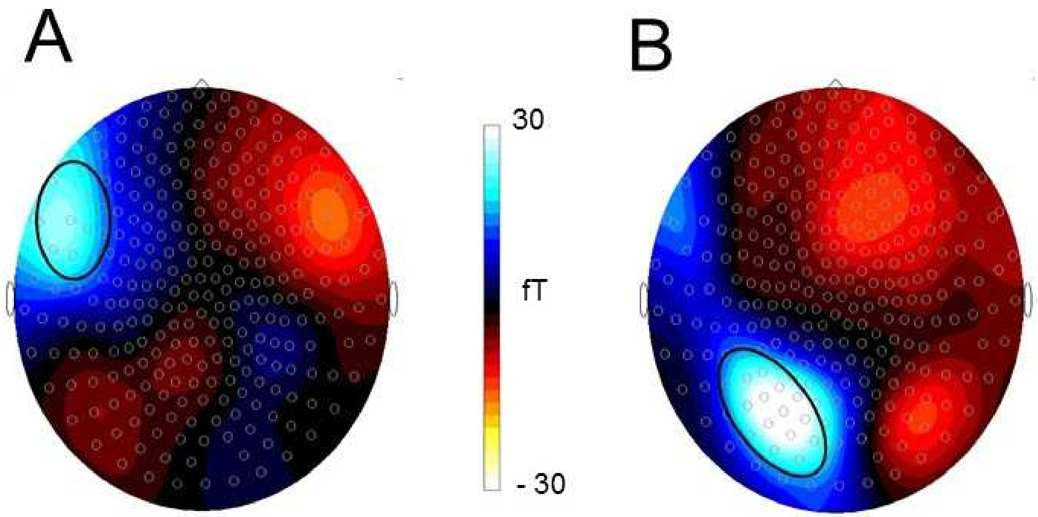
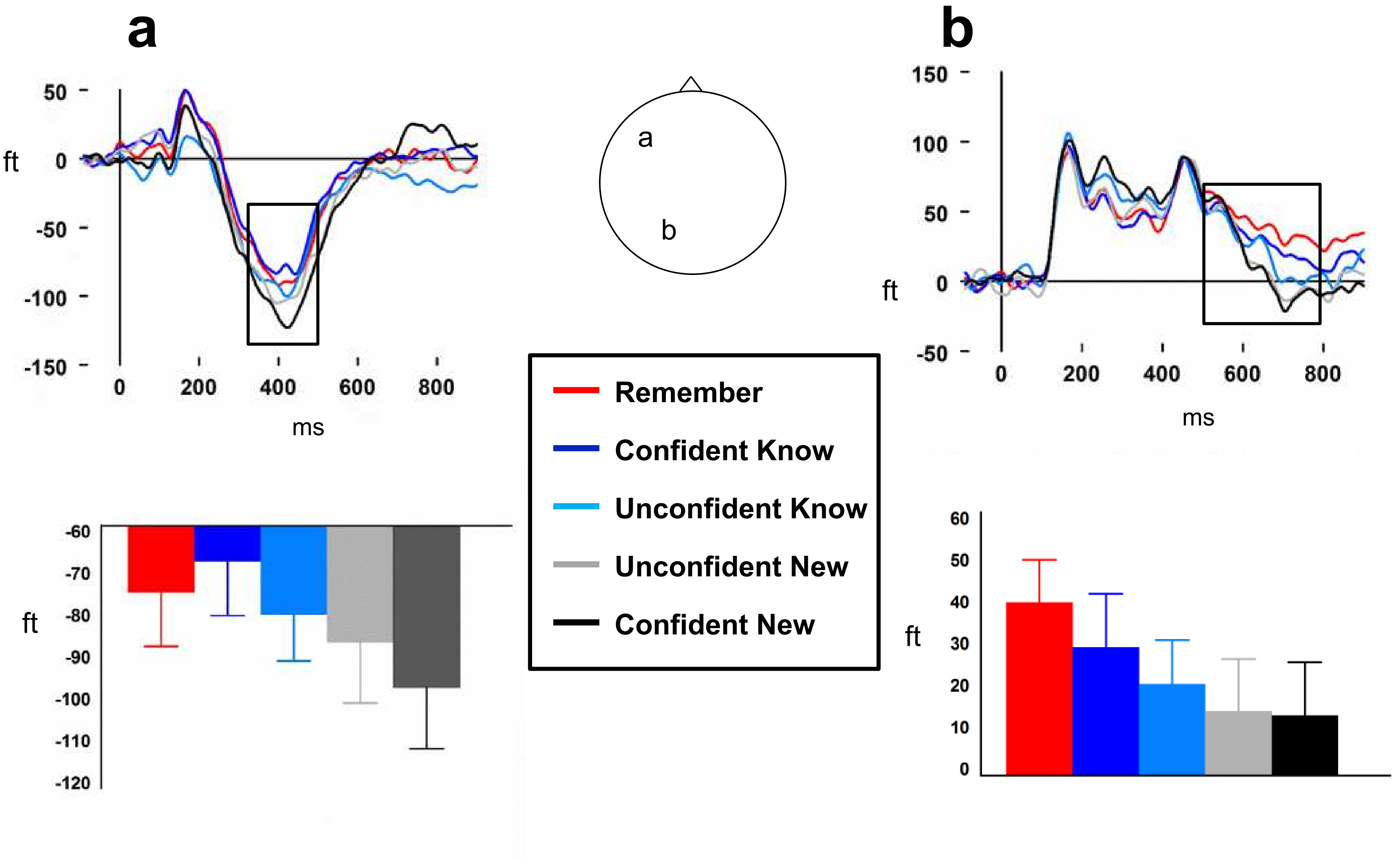


Figure 2


a
b
50
0
-50
-100
-150
ft
0
200
400
600
800
ms
150
100
50
0
-50
ft
0
200
400
600
800
ms
Remember
Confident Know
Unconfident Know
Unconfident New
Confident New
-60
-70
-80
-90
-100
-110
-120
ft
60
50
40
30
20
10
0
ft