

The FN400 is functionally distinct from the N400

Emma K. Bridger^{a,*}, Regine Bader^a, Olga Kriukova^a, Kerstin Unger^b, Axel Mecklinger^a

^a Experimental Neuropsychology Unit, Department of Psychology, Saarland University, 66123 Saarbrücken, Germany

^b Unit for Development of Language, Learning and Action, Department of Psychology, Saarland University, 66123 Saarbrücken, Germany

ARTICLE INFO

Article history:

Accepted 18 July 2012

Available online 28 July 2012

Keywords:

Familiarity

Event-related potentials

FN400

N400

Semantic priming

Recognition memory

ABSTRACT

The FN400 refers to the early midfrontally-distributed difference between ERPs elicited by old and new items, which operates in a way consistent with a neural marker of familiarity-based recognition. Double dissociations between the FN400 and a later ERP index of recollection provide some of the most compelling evidence in support of dual-process models to date. It has recently been claimed, however, that there is no evidence that the FN400 is functionally distinct from the N400 index of implicit semantic priming (Voss, J., and Federmeier, K., FN400 potentials are functionally identical to N400 potentials and reflect semantic processing during recognition testing, *Psychophysiology*, 48, 532–546, 2011), challenging inferences made on the basis of this effect. We argue that the design employed to make this claim is flawed because it comprised a semantic priming manipulation embedded within a continuous recognition test which enabled recognition contrasts to be confounded by semantic processes in a number of ways. Here, ERPs were recorded from a design which avoided these confounds by employing a semantic priming paradigm which also served as the encoding phase for a surprise subsequent recognition test phase. An N400 effect elicited in the semantic priming task demonstrated the established centro-parietal maximum, whereas the difference between correctly responded to old and new ERPs in the recognition test was maximal over frontal sites in the same time window. When direct comparisons of the electrophysiological correlates of semantic priming and episodic recognition are recorded in a paradigm in which the two are not confounded, the FN400 reflects a qualitatively distinct effect from the N400.

© 2012 Elsevier Inc. All rights reserved.

Introduction

Event-related potential (ERP) old/new effects, the differences between ERPs elicited by correctly classified old and new items presented in episodic recognition tasks, provide indices of successful retrieval and associated downstream processes. Across recognition memory studies, ERP old/new effects have been shown to differentiate from one another by virtue of their sensitivity to particular experimental variables, alongside the temporal, morphological and topographical characteristics unique to each effect (Wilding and Herron, 2006). Two old/new effects have garnered particular attention because they consistently behave in a way that converges with dual-process models of recognition memory, which state that recognition judgments can be supported by two independent processes: familiarity, a strength-like indicator of previous occurrence and recollection, a later-occurring process that supports the retrieval of explicit contextual details (e.g. Mandler, 1980; Yonelinas, 2002; Yonelinas et al., 2010). The first of these old/new effects is maximal over frontal sites between 300 and 500 milliseconds (ms) post-stimulus, and is correspondingly termed the early midfrontal old/new effect. This

effect is often associated with familiarity-based recognition because, while it varies linearly with familiarity strength (Woodruff et al., 2006; Yu and Rugg, 2010), it does not distinguish correctly responded to old items and familiarity-based false alarms (Curran, 2000; Curran and Cleary, 2003; Nessler et al., 2001) or items associated with different degrees of recollective experience (Vilberg et al., 2006).

The second of these old/new effects typically occurs around 500–700 ms and is termed the left parietal old/new effect because of the scalp sites over which it is maximal. The parietal effect consistently behaves as an electrical marker of recollection, distinguishing, for example, old items for which associated source information was either correctly or incorrectly retrieved (Wilding and Rugg, 1996; Wilding et al., 1995). Moreover, the amplitude of the left parietal effect correlates with the number of correctly retrieved contextual details (Vilberg and Rugg, 2009; Wilding, 2000) and maps onto phenomenological reports of recollection-based recognition (e.g. Woodruff et al., 2006). The chronology of the two ERP effects also corresponds with the time course of familiarity and recollection as revealed by behavioral studies employing response deadline manipulations (e.g. McElree et al., 1999, also see Sauvage et al., 2010, for comparable data in rats). The direct insight into recognition processes that ERP old/new effects provide in this manner has played an important role in moving the single vs. dual-process debate beyond the relative impasse reached on the basis of behavioral models alone (Donaldson and Curran, 2007). In accordance with this

* Corresponding author at: Department of Psychology, Saarland University, 66123 Saarbrücken, Germany.

E-mail address: e.bridger@mx.uni-saarland.de (E.K. Bridger).

is the significance bestowed upon those reports in which manipulations have been shown to doubly dissociate the midfrontal and left parietal old/new effects, in line with the presence of two qualitatively distinct processes which can contribute to recognition judgments (Curran and Doyle, 2011; Jäger et al., 2006; Stenberg et al., 2009; Woodruff et al., 2006). While the compelling amount of convergent animal and functional imaging data cannot be ignored (e.g. Brown and Aggleton, 2001; Sauvage et al., 2010; Skinner and Fernandes, 2007), it is ERP data points which provide some of the most unequivocal support for dual-process models of recognition memory to date (Donaldson and Curran, 2007).

The significance of these dissociations has been challenged, however, by the recent claim that there is no evidence that the midfrontal old/new effect is functionally and electrophysiologically distinct from N400 modulations that are observed in semantic priming paradigms (Voss and Federmeier, 2011). The N400 is a negative-going component that peaks over centro-parietal sites around 400 ms post-stimulus, which consistently operates as a marker of the degree of semantic processing (Kutas and Hillyard, 1980; Kutas and Federmeier, 2000, 2010). The similarity in time course and morphology of the two effects has led some to employ the term FN400 for the midfrontal old/new effect, where the 'F' signifies the more frontal distribution of the effect observed in episodic recognition studies (Curran, 1999). The claim that there is no functional distinction between the FN400 and the N400 represents the latest in a series of reports in which it is argued that the FN400 reflects conceptual priming rather than familiarity (e.g. Paller et al., 2007; Voss et al., 2010; Yovel and Paller, 2004). Data points held in support of this position have stressed the sensitivity of early frontal potentials to conceptual priming when familiarity is ostensibly controlled (see Discussion for further elaboration). According to Voss and Federmeier, the frontal distribution of the recognition old/new effect arises by virtue of the particular stimuli employed in recognition studies rather than the engagement of processes functionally distinct from those indexed by the N400.

To test the relationship between the FN400 and the N400, Voss and Federmeier compared the two effects using a semantic priming manipulation embedded within a continuous recognition task. Throughout the task, critical test words were repeated once and were primed by a semantically-related preceding item on either their first or second presentation. Upon the presentation of each item, participants made an initial valence judgment and then a subsequent remember/know/new episodic judgment (e.g. Gardiner, 1988). ERPs associated with items that were not semantically primed were separated according to whether they were elicited on the first or second presentation. This comparison was assumed to provide a contrast analogous to the standard ERP old/new effect observed in most recognition studies. Differences between these items from 300 to 500 ms were found to be electrophysiologically indistinguishable from the semantic priming contrast, which was operationalized as the ERP difference between primed words on their first presentation and the preceding related prime. Thus, on the basis of the null outcomes of topographical comparisons between these contrasts, the authors claimed that the FN400 is functionally identical to the N400 and that conceptual priming which occurs throughout recognition tasks elicits an N400 which has been consistently misinterpreted as the midfrontal old/new index of familiarity.

Several consequences that follow from manipulating semantic priming within a recognition task, however, critically undermine Voss and Federmeier's assumption that comparing the first and second presentations of unprimed words indexes familiarity-based recognition as it is typically observed in episodic recognition memory paradigms. Consider first that although critical 'old' items were not primed at the point from which recognition contrasts were taken, they had nonetheless been recently primed on their initial presentation approximately 15–25 items previously. This interval between

first and second presentation is notably shorter than that employed in standard recognition paradigms and one consequence may be that the electrophysiological indices of recently priming these items remain observable on their second presentation. The prime-target semantic association could, for example, be reactivated on the subsequent presentation of each target. Put another way, we question the validity of using recently semantically primed targets in an old/new recognition contrast designed to investigate whether early recognition reduces to priming processes, when the two processes are confounded with one another.

There is an alternative route by which the semantic priming manipulation may have directly encroached upon the old/new recognition contrast and this arises from the possibility that it encouraged participants to generate semantic expectancies which, when violated, would lead to larger N400 potentials. The high proportion of items that were preceded by a semantically related prime is likely to have alerted participants to the semantic nature of the task. Moreover, the long inter-stimulus interval (approximately 5 s) that arose following the double response requirement is likely to account for the absence of the standard behavioral priming effect usually observed in semantic priming tasks, but more crucially, it increases the opportunity for participants to develop expectancies about the semantics of each item on the basis of the preceding stimulus. Strategic semantic processes are thought to increase with longer stimulus onset asynchronies (Neely, 1977), and it is relatively clear that the N400 at least in part reflects controlled semantic processing such as the development of expectancies. This is most clearly illustrated by the inverse relationship between N400 amplitude and the contextual expectancy of words (Kutas and Hillyard, 1984; Lau et al., 2008). In the case of unprimed items these expectancies will inevitably be violated and are subsequently likely to be associated with relatively larger N400 potentials. This is particularly important because many of these unprimed items operated as baseline 'new' items for the recognition contrast, and the possibility that they could be associated with enhanced N400 potentials makes them inappropriate for an episodic 'old/new' contrast.

Alongside these concerns, arise others pertaining to the particular response requirements employed – to evaluate semantic features of items before making an episodic judgment – a constraint which deviates considerably from typical episodic task requirements. Changes in retrieval task requirements can influence the pattern and distribution of early old/new effects as shown by one study in which implicit vs. explicit episodic retrieval requirements modulated the pattern and distribution of early old/new effects (Küper et al., 2012). Likewise, it is possible that the combination of semantic and episodic response requirements in the Voss and Federmeier study modulated the signal that participants assessed during the critical ERP recording period.

Together, these observations underscore important ways in which the demands of the task reported by Voss and Federmeier differ considerably from those assumed to underlie familiarity-based recognition by confounding it with semantic processing. In order to properly compare the distribution of these two effects, care must be taken to ensure that contrasts encapsulate the operations traditionally assumed to support semantic priming and recognition, respectively. This was achieved in the current study by separating the phases under which semantic priming and recognition were assumed to be elicited and subsequently measured via ERPs. Participants completed an incidental study phase in which they had to make valence judgments to a series of words. One half of the target items presented in this phase were preceded by a semantically related prime while items from the remaining half were preceded by an unrelated item. Comparing ERPs elicited by these two classes of targets provided the classic index of semantic priming (Kutas and Federmeier, 2010). Twenty-five minutes later, participants completed a surprise recognition test which contained unprimed targets from the first phase intermixed with completely new items, and

were required to make a simple old/new response to each item.¹ ERP differences elicited by correctly responded to old and new items between 300 and 500 ms were presumed to provide a reliable index of familiarity-based recognition because (i) old items were not semantically primed upon initial presentation in the study phase, (ii) recognition-related processing of items was not confounded by semantic expectancy and (iii) participants were only required to make a simple episodic judgment to each of these items. The distribution of the differences between these ERPs from 300 to 500 ms was predicted to have a midfrontal maximum, in line with the standard signature of familiarity-based recognition, which should be topographically distinct from the centro-parietally distributed N400 recorded during the study/priming phase.

Methods

Participants

Twenty native German speakers (10 male) were recruited from the student population of Saarland University. All were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) and had no known neurological problems. The mean age of participants was 25 years (range = 21–31 years). Informed consent was required, payment was provided at a rate of €8/h, and participants were debriefed after the experiment. The experiment was approved by the local ethics committee of Saarland University. A further 2 students also participated but were excluded from the final analyses because they either failed to follow instructions or had a discrimination value ($p[\text{hit}] - p[\text{false alarm}]$) close to zero.

Stimuli and design

Stimuli were 165 semantically associated German word pairs, each comprising a target and an associated prime, both of which were concrete nouns. Approximately 200 pairs were initially derived using the Edinburgh Associative Thesaurus (Kiss et al., 1973) to develop a stimulus set with standardized forward association strengths. Pairs were translated into German and the presence of semantic associations was verified by three independent native German speakers. The mean EAT word association value for the 165 targets remaining after this procedure was 0.17 (range = 0.01–0.71). Association values derived from the Noun Associations for German database (Melinger and Weber, 2006) were available for a subset of 40 word pairs, and these corresponded with the values derived from the EAT (mean forward association strength = 0.17; range = 0.03–0.31). Targets were within a normal frequency range (mean Mannheim frequency = 75 occurrences per million; range = 11–421; Baayen et al., 1993) and were between 3 and 11 characters in length. Concreteness values were derived from English translations of words taken from the MRC psycholinguistic database (mean target concreteness = 498, range = 258–638). Stimuli were presented in the center of the screen in black on a gray background. The vertical visual angle subtended 1.1° and the horizontal visual angle was between 3.3 and 8.9° (at a viewing distance of 70 cm).

Word pairs were allocated to three lists of 55, each matched for word length, frequency and concreteness of both the prime and of the target, as well as for the two measures of the strength of association. A second version of each list was created by randomly reallocating targets to unrelated primes. This ensured that, across subjects, all pairs could be presented in both primed and unprimed conditions ensuring that any differences between these conditions could not be attributed to

stimulus-specific attributes (Küper and Heil, 2010; Raaijmakers et al., 1999). In the study/priming phase, one list of related pairs and one list of unrelated pairs were presented, pseudo-randomly intermixed with one another. At test, the 55 targets from the unrelated condition were re-presented along with 55 new items, which comprised the targets from the third list. Rotating lists across participants therefore ensured that targets were counterbalanced across the primed, unprimed and new item conditions.

Procedure

The overall experimental design is outlined in Fig. 1. Each experimental session began with the fitting of the electroencephalogram cap (see parameters below). The experiment tasks began with an incidental study/priming phase. Participants were informed that they would see a series of words presented on the screen and that they were required to make a binary pleasant/unpleasant distinction to each word with the index finger of each hand using the buttons 'c' or 'm' on a standard keyboard. 50% of the participants made the response "pleasant" using the left index finger. Before beginning the study phase proper, participants performed a short practice phase comprising 6 word pairs in order to acquaint them with the timing of the study phase. Each study trial began with a fixation cross for 500 ms which was replaced by the prime of each pair for 300 ms. The screen was then blanked for a 1000 ms response interval, before a fixation cross was presented for 500 ms and the target appeared for 300 ms. Trials appeared in a continuous fashion with an SOA of 1800 ms. During the practice phase, the 1000 ms response screen indicated whether the 'c' or 'm' button specified the pleasant or unpleasant judgment but this information was absent during the task proper. Participants took a self-paced break midway through the study phase.

After the study/priming phase, participants completed two distractor tasks: an automated version of the Ospan task of working memory (Unsworth et al., 2005) and a visual oddball task. In total, these tasks required 20–25 min to complete and were included to ensure that the final recognition task was not too easy by maintaining a delay between study and test. The data from these tasks are not considered further here. In the final phase, participants were asked to complete an old/new

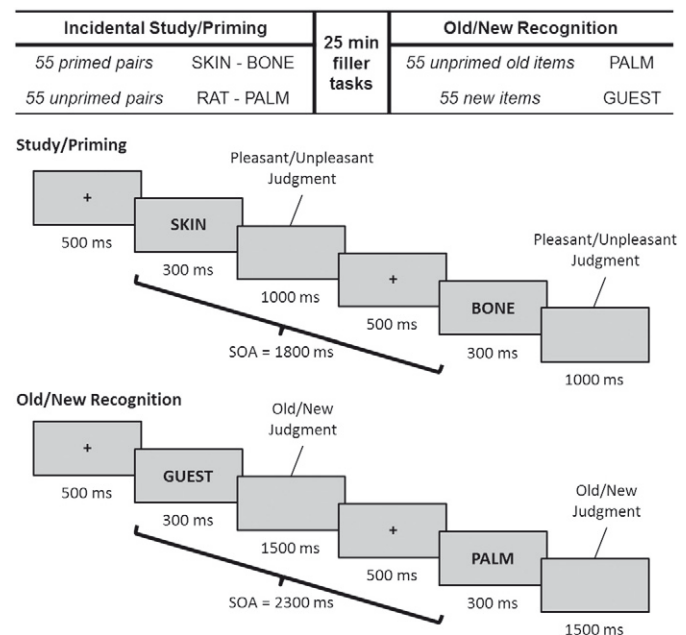


Fig. 1. Upper panel: diagram of the experimental design. Words comprise English translations of selected German words from the original stimulus set. Lower panels: schematic illustration of the trial parameters employed in the two task phases.

¹ This differs from the requirements employed by Voss and Federmeier because, although response judgments such as the remember/know distinction can dissociate different aspects of episodic experiences, they cannot provide any direct insight into the principal concern of the current design: assessing the relationship between early components of the electrical record across semantic and episodic tasks.

recognition test for the items they saw during the study phase, after completing a short practice test (6 items). Test trials began with a fixation cross for 500 ms, which was replaced by the target word for 300 ms and a blank screen for 1200 ms, during which participants were required to make a simple old/new binary judgment. The mapping of old/new responses onto left:right ('c':'m') buttons was counterbalanced across participants. Participants took another self-paced break midway during the test phase.

Electrophysiological recording parameters and analyses

Continuous EEG was recorded from 58 scalp locations based on the extended international 10–20 system (Jasper, 1958). EEG was acquired referenced to the left mastoid and re-referenced off-line to the average of the mastoid signals. EEG signals were band-pass filtered from DC–250 Hz and digitized at a sampling rate of 500 Hz. Electro-oculographic activity (EOG) was assessed using signals recorded from four additional electrodes above and below the right eye (vertical EOG) and on the outer canthi (horizontal EOG). Electrode impedances were kept below 5 k Ω . Offline, a digital band-pass filter (0.03–30 Hz) was applied and epochs were created beginning 100 ms prior to and ending 1000 ms after the onset of stimulus presentation. Waveforms were corrected relative to the 100 ms pre-stimulus baseline period. EOG blink and movement artifacts were corrected using the modified linear regression algorithm (Gratton et al., 1983) embedded in the EEProbe software package.

Analyses were focused upon a selection of electrodes encompassing a dense array of sites taken from frontal (F3, F1, Fz, F2, F4), fronto-central (FC3, FC1, FCz, FC2, FC4), central (C3, C1, Cz, C2, C4), centro-parietal (CP3, CP1, CPz, CP2, CP4) and parietal (P3, P1, Pz, P2, P4) locations, selected in order to adequately cover the principal scalp sites of interest. Mean amplitude values were taken from the 300–500 ms time window to quantify the N400 and midfrontal old/new effect respectively. Inferential statistics were conducted using multivariate analyses of variance (MANOVAs) in line with the invulnerability of this approach to violations in sphericity (Dien and Santuzzi, 2005; Picton et al., 2000). MANOVAs included location factors of anterior–posterior (ant–post: frontal, fronto-central, central, centro-parietal, parietal) and sagittal plane (SP: left midlateral, left superior, midline, right superior, right midlateral). Level of SP factor corresponded to the electrode nomenclature in the following ways: 3 = left midlateral, 1 = left superior, 2 = midline, 4 = right superior and 5 = right midlateral. An analysis of this kind, in which a dense set of electrodes were employed while location factors were crossed entirely, should allow detection of even subtle differences in distribution. Holm's sequential Bonferroni correction (Holm, 1979) was applied to correct for multiple comparisons in follow-up MANOVAs and the significance level was set to $\alpha = .05$. Critical topographic analyses were conducted on both unscaled and rescaled data and the vector length procedure was employed for rescaling (McCarthy and Wood, 1985; Picton et al., 2000). Although this procedure is not without criticism (Urbach and Kutas, 2006), the main concerns associated with this procedure are reduced considerably when rescaling is applied to subtraction waveforms, as was the case here (Wilding, 2006). The mean proportion of artifact-free trials contributing to individual subject grand averages for each of the four conditions was as follows: primed = 37 (range 23–51), unprimed = 38 (range 26–54), hits = 33 (range 20–48) and correct rejections = 29 (range 19–41).

Results

Behavior

Participants were significantly quicker to make a pleasantness judgment to targets preceded by a semantically related prime (mean = 685 ms, SD = 118 ms) than those preceded by an unrelated

prime (mean = 713 ms, SD = 120 ms; $t(19) = 4.57$, $p < .001$). Participants failed to provide a response before the onset of the next trial on an average of .03 (SD = .05) of study trials, and these time-out trials were excluded from all analyses. During the test phase, participants were more likely to make a correct response to an old item (mean = .81, SD = .11) than to a new item (mean = .73, SD = .08) yielding a mean $Pr(p[\text{hit}] - p[\text{false alarm}])$; Snodgrass and Corwin, 1988) of .54 (SD = .13). Correct responses to old items were significantly faster (mean = 752 ms, SD = 102 ms) than to new items (mean = 815 ms, SD = 108 ms, $t(19) = 5.22$, $p < .001$). The mean proportion of trials in which participants failed to respond before the onset of the next test trial was .02 (SD = .02). Response bias ($p[\text{false alarm}]/(1 - Pr)$; Snodgrass and Corwin, 1988) was relatively liberal as indicated by a mean Br of .60 (SD = .15).

ERPs

Fig. 2A depicts grand average ERPs elicited by words presented in the study phase separated according to whether they were preceded by a semantically related (primed) or unrelated (unprimed) word. ERPs diverge around 300 ms post-stimulus, when the negative-going N400 component is greater for unprimed items. This relative negativity peaks at 400 ms and extends across all scalp sites until approximately 600 ms, although it is largest at central and centro-parietal sites. Fig. 2B depicts the grand average ERPs elicited by correctly responded to old (hits) and new (correct rejections) words presented in the test phase. ERPs elicited by correct rejections become more negative than hits from approximately 300 ms post-stimulus, with a negative peak at 400 ms and remain relatively negative compared to hit ERPs until the end of the recording epoch, particularly over frontal sites. Although the relative negativity in the critical 300–500 ms time window extends to posterior sites, it is notably largest at frontal and fronto-central sites.

Inferential analyses on these data began with a comparison between primed and unprimed ERPs from 300 to 500 ms using a MANOVA with factors of priming (primed, unprimed), ant–post (frontal, fronto-central, central, centro-parietal, parietal) and SP (left midlateral, left superior, midline, right superior, right midlateral) and revealed a main effect of priming ($F(1,19) = 54.06$, $p < .001$) and an interaction between priming and ant–post ($F(4,16) = 3.80$, $p < .05$). The priming \times ant–post interaction was deconstructed via pairwise comparisons on adjacent levels of ant–post. This revealed a reliable interaction between priming and ant–post for the contrast between frontal and fronto-central levels ($F(1,19) = 12.79$, $p < .01$). There were no other interactions including the priming and ant–post terms for the remaining contrasts (corrected $ps > .20$). The amplitude of the ERP priming difference thus comprised a broadly-distributed plateau over central and parietal sites which decreased in amplitude from fronto-central to frontal sites.

Comparisons between hit and correct rejection ERPs from 300 to 500 ms employed a MANOVA with factors of item type (hit, correct rejection), ant–post (5 levels) and SP (5 levels) and revealed a main effect of item type ($F(1,19) = 35.20$, $p < .001$), an interaction between item type and ant–post ($F(4,16) = 5.55$, $p < .01$) and an interaction between all three factors ($F(4,16) = 6.60$, $p < .05$). The three-way interaction was deconstructed by making pairwise comparisons with the factors of item type (2), ant–post (2) and SP (5) for adjacent levels of ant–post. This revealed reliable interactions between item type, ant–post and SP ($F(4,16) = 7.45$, $p < .01$) when frontal and fronto-central levels were contrasted, and a marginally significant interaction with the same terms for the fronto-central vs. central contrast ($F(4,16) = 3.67$, $p = .08$). This pattern is in line with a change in lateralization of the old/new effect (with a presumed focus over midline and right superior sites) which was most pronounced at fronto-central sites.

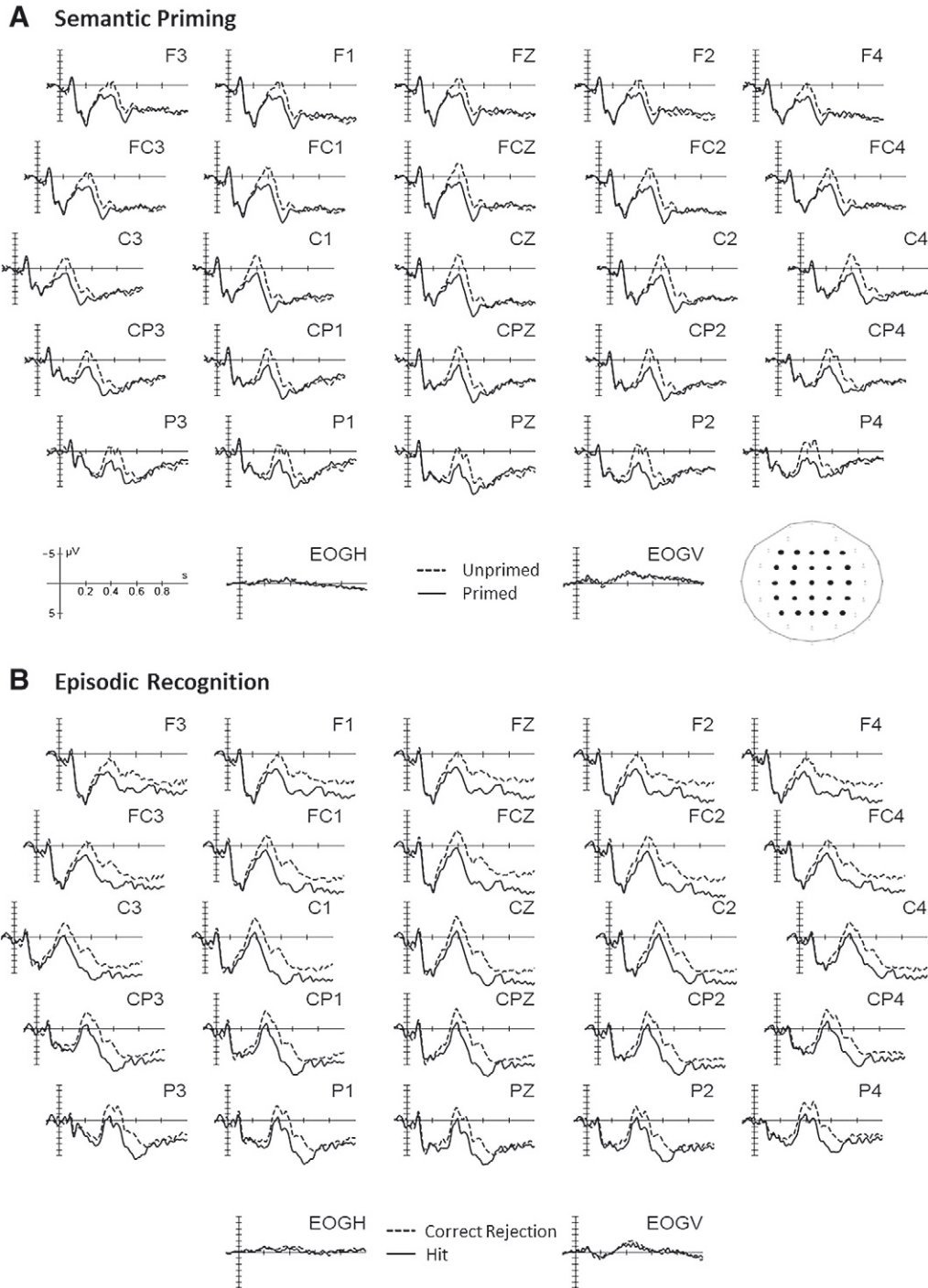


Fig. 2. A. Grand average ERPs elicited by primed and unprimed targets in the study/priming phase. Data are shown for the 25 electrode locations used in all analyses at frontal (F3, F1, Fz, F2, F4), fronto-central (FC3, FC1, FCz, FC2, FC4), central (C3, C1, Cz, C2, C4), centro-parietal (CP, CP1, CPz, CP2, CP4) and parietal (P3, P1, Pz, P2, P4) scalp sites. Grand average ERPs are also shown for the horizontal and vertical EOG channels. B. Grand average ERPs elicited by hits and correct rejections in the recognition test phase at the 25 electrode sites used in all analyses.

The outcomes of the preceding analyses reveal robust and widely distributed differences between ERPs from 300 to 500 ms in both phases. Moreover, they indicate that the amplitude of these effects was greater over some scalp sites than others and, critically, that this pattern was different for the two contrasts: whereas the priming effect was largest over central and posterior sites, the recognition old/new effect revealed a midline-to-right fronto-central topographic distribution. This pattern is illustrated in Fig. 3, which shows that whereas the scalp topography of the priming effect elicited in the study phase comprised a centro-parietal maximum, the early old/new effect

elicited in the recognition test phase demonstrated an effect with a pronounced midline-to-right distribution at fronto-central recording sites. The critical test of the current experiment was to determine whether the distribution of these effects differ significantly from one another. Thus, the subtraction values akin to the mean subtractions depicted in the scalp maps in Fig. 3 were submitted to a MANOVA with factors of subtraction contrast (priming, recognition), ant-post (frontal, fronto-central, central, centro-parietal, parietal) and SP (left midlateral, left superior, midline, right superior, right midlateral), which elicited an interaction between subtraction

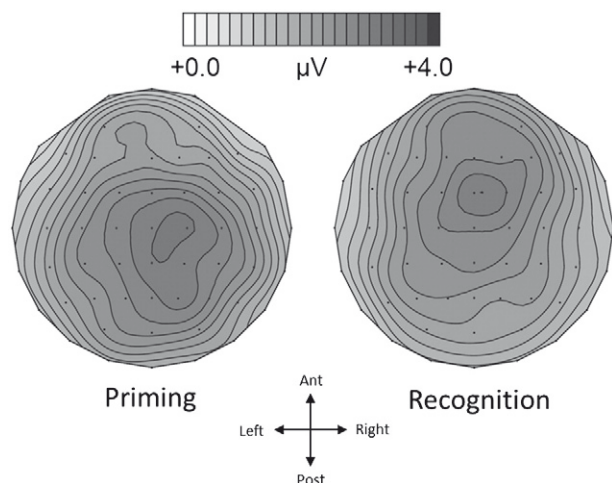


Fig. 3. Topographic maps showing the scalp distributions of the differences between ERPs associated with the two critical contrasts. For the priming contrast, unprimed ERPs were subtracted from primed ERPs. For the recognition contrast, correct rejection ERPs were subtracted from hit ERPs. Maps are computed on the basis of the mean difference scores taken from the 300–500 ms time window and are both depicted along the same scale (see grayscale bar).

contrast and ant–post ($F(4,16) = 3.30$, $p < .05$). This interaction term remained significant ($F(4,16) = 3.46$, $p < .05$) when the subtraction values were rescaled. Thus, the anterior/posterior distributional differences between the two contrasts depicted in Fig. 3 reflect the engagement of distinct electrophysiological patterns of activity.

A final set of analyses were conducted in the subsequent 500–700 ms epoch in order to characterize the later old/new effect of recollection. Hit and correct rejection ERPs from this epoch were submitted to a MANOVA with factors of item type (hit, correct rejection), ant–post (5 levels) and SP (5 levels) and revealed a main effect of item type ($F(1,19) = 30.27$, $p < .001$) which was moderated by interactions between item type and ant–post ($F(4,16) = 3.16$, $p < .05$) and between item type and SP ($F(4,16) = 4.54$, $p < .05$). Follow-up comparisons revealed main effects of item type at all 5 levels of ant–post (frontal, $F(1,19) = 30.48$, $p < .001$; fronto-central, $F(1,19) = 30.44$, $p < .001$; central, $F(1,19) = 29.31$, $p < .017$; centro-parietal, $F(1,19) = 24.92$, $p < .001$; parietal, $F(1,19) = 18.58$, $p < .001$) and at all levels of SP (left midlateral, $F(1,19) = 32.37$, $p < .001$; left superior, $F(1,19) = 34.83$, $p < .001$; midline, $F(1,19) = 28.76$, $p < .001$; right superior, $F(1,19) = 23.80$, $p < .001$; right midlateral, $F(1,19) = 21.36$, $p < .001$). These outcomes indicate that old/new effects in this time window were greatest over left hemisphere sites and at fronto-central and central sites. This left fronto-central to central distribution differs from the left parietal maximum pattern typically reported in this time window. However, the later 500–700 ms was more posterior and left lateralized than the early midfrontal old/new effect. This change in distribution from the early to the late time window was confirmed with analyses of the subtraction values submitted to a MANOVA with factors of subtraction contrast (300–500, 500–700), ant–post (5 levels) and SP (5 levels). Subtraction contrast interacted with ant–post ($F(4,16) = 4.73$, $p < .05$) and this interaction term remained after the data had been rescaled ($F(4,16) = 4.97$, $p < .01$). The current data are thus in line with the engagement of qualitatively distinct recognition processes in the 300–500 and 500–700 time windows.

Discussion

A simple study-test paradigm was employed in which the electrophysiological correlates of semantic priming and episodic recognition were recorded in separate phases, ensuring that the one did not impact upon the processing engaged during the other. Comparisons between semantically primed and unprimed items in the study phase revealed

behavioral evidence of priming, alongside a modulation of the N400 effect. In line with the characteristic N400 observed for word stimuli (Kutas and Federmeier, 2010), this effect was greater for unprimed items, peaked at around 400 ms post-stimulus and showed a centro-parietal scalp distribution. Robust ERP old/new effects were observed in the subsequent recognition test phase and the distribution of the old/new effect in the critical 300–500 ms time window demonstrated a midline to right fronto-central distribution. It was also topographically distinct from the old/new effect in the subsequent 500–700 ms time window as would be expected if two qualitatively distinct processes contribute to recognition memory (Rugg and Curran, 2007). Of most importance was the observation that there was a significant difference in the topography of the recognition old/new effect and the N400 in the 300–500 ms time window. This demonstration speaks directly against the claim that the FN400 reduces to the N400 (Voss and Federmeier, 2011) instead showing that functionally distinct processes are engaged between 300 and 500 ms post-stimulus depending upon whether stimuli vary in familiarity or the extent to which they have been primed by a semantic associate. We argue that Voss and Federmeier (2011) failed to observe this distinction because the design they employed confounded episodic recognition with semantic processing in a number of ways. In particular, N400 potentials for new items may have been greater than is typically observed in recognition tasks as a consequence of violations in semantic expectancy and this may have pushed the distribution of the ‘old/new’ effect towards a more posterior maximum. Moreover, it is not possible to exclude the possibility that recognition contrasts also indexed semantic priming because old items had recently been semantically primed. When recognition contrasts were made without these confounds in the current experiment, the early old/new effect showed the expected midfrontal distribution which was distinct from the N400 semantic priming effect.

Observing that different experimental manipulations are associated with ERP effects with distinct scalp topographies is a necessary but not a sufficient precondition for inferring the engagement of distinct cognitive mechanisms in each condition. It is conceivable, for example, that distinct stimuli might elicit non-overlapping scalp distributions in comparable tasks, not necessarily because of changes in the cognitive operations engaged but because the representations of the stimuli employed may not overlap entirely with one another (Rugg and Coles, 1995). We assume that it is changes of this kind which Voss and Federmeier allude to when noting the sensitivity of the N400 distribution to particular stimuli manipulations. In particular, they note that the N400 has been shown to be more frontally distributed for concrete stimuli (e.g. Kounios and Holcomb, 1994) such as are typically employed in recognition studies and that this might account for the midfrontal distribution observed in these studies. The current data strongly speak against such an account, however, because while stimuli employed in the current experiment comprised concrete nouns, the semantic priming N400 effect demonstrated the standard centro-parietal distribution. The early ERP old/new effect associated with later recognizing these same items however showed the standard frontal distribution. Thus, while stimuli were held constant, changes in functional task demands – whether stimuli vary in episodic memory strength or the extent to which they have been primed by a semantic associate – were associated with distinct patterns of electrophysiological activity.

The claim that there is no functional distinction between FN400 and N400 processing has been taken as evidence for the view that the FN400 comprises an index of conceptual priming rather than explicit familiarity (see Paller et al., 2007 for a review). Support for this perspective comes from demonstrations that early midfrontal ERPs distinguish stimuli which differentially support conceptual priming in independent behavioral studies (Voss and Paller, 2007; Voss et al., 2010). These contrasts represent necessary contributions to the understanding of FN400 functionality but do not provide unequivocal evidence that the

FN400 indexes implicit conceptual priming rather than explicit familiarity. Firstly, there remain a number of data points which simply cannot be accommodated within a pure conceptual priming account of the FN400. These comprise the increasing number of demonstrations in which the effect has been shown to vary with the degree of perceptual overlap between items at study and test while conceptual processing presumably remains unchanged (Curran and Doyle, 2011; Ecker and Zimmer, 2009; Ecker et al., 2007; Groh-Bordin et al., 2005, 2006; Küper et al., 2012; Schloerscheidt and Rugg, 2004). A second point is that although priming and recognition appear to be dissociable under some circumstances (e.g. Voss and Gonsalves, 2010), it has nonetheless proven difficult to convincingly demonstrate that behavioral estimates of familiarity can be equated for stimuli which differentially support conceptual priming (see Grove and Wilding, 2009, for full argument). The difficulty of fully dissociating familiarity and implicit conceptual priming in this manner is in line with the notion that the two processes may rely on a common fluency process (Wagner and Gabrieli, 1998; Yonelinas, 2002) and/or depend upon a common neural generator (Wang et al., 2010).

Such an account assumes a degree of overlap in the neural generators responsible for familiarity and conceptual priming. The usual restrictions apply when making claims about the likely neural generators of scalp-recorded ERP effects, but there is convergent evidence that anterior medial temporal lobe (aMTL) structures are necessary for both semantic priming and familiarity-based recognition. Intracranial N400-like effects have been recorded within aMTL structures following both semantic priming (Nobre and McCarthy, 1995) and semantic violation manipulations (McCarthy et al., 1995; Meyer et al., 2005) and this corresponds with fMRI studies which have reported modulations in aMTL regions using semantic priming (Rossell et al., 2003) and semantic violation paradigms (Meyer et al., 2010). Critically, hemodynamic activations in this area consistently map onto familiarity in episodic recognition studies (e.g. Henson et al., 2003). Moreover, aMTL lesions are associated with selective deficits in familiarity-based recognition (Bowles et al., 2007) and implicit conceptual priming (Wang et al., 2010). If aMTL structures play a role in both semantic priming and episodic familiarity, which brain regions are likely to be responsible for the characteristic midfrontal distribution of the early old/new effect observed in most recognition studies? One candidate region which corresponds broadly with the scalp distribution of the FN400 is the bilateral dorsolateral prefrontal cortex. Activation in dorsolateral prefrontal cortex during recognition tasks shows a linear sensitivity to the confidence of familiarity-based recognition responses (Yonelinas et al., 2005) and lesions to this area have recently been associated with selective familiarity deficits while recollection remains unimpaired (Aly et al., 2011; MacPherson et al., 2008). It remains to be shown however whether the role of lateral prefrontal cortices maps onto the time course of the early midfrontal old/new effect, but insofar as familiarity is thought to require the on-line checking of memory strength against decision criteria (Yonelinas, 2002), it remains reasonable to posit a significant role for the prefrontal cortex in episodic familiarity.

The electrophysiological dissociation shown here and the majority of midfrontal old/new data points reviewed above justify to some extent the distinctions that have been made in the respective ERP language and recognition memory literatures to date. This does not, however, preclude the possibility that under some circumstances, changes in semantic processing reflected in N400-type old/new effects might be used to guide responses in recognition tasks. Patterns of this kind have, for example, been reported in one recent associative memory paradigm in which the correct recognition of unitized items was associated with an early posterior old/new effect reminiscent of the N400 (Bader et al., 2010). These items were unitized at study by way of a definition encoding task which provided them with a novel semantic entry. The early posterior old/new effect at test was assumed to arise because of the conceptual fluency elicited by these items at test relative to non-integrated new pairs. This effect was

replicated in a second report of this kind, in which it was dissociated from the early midfrontal old/new effect elicited by the correct recognition of these same items presented in reverse order, in order to break-up the new unitized conceptual representation while leaving item familiarity intact (Wiegand et al., 2010). In light of the caveats associated with interpreting changes in scalp topography, it remains to be shown whether these posterior effects reflect episodic memory processes engaged for pre-experimentally unfamiliar stimuli or a change in reliance of the kind of processing signal engaged, but this pattern nonetheless indicates that distinct electrophysiological effects can be associated with comparable response outcomes. Co-occurring midfrontal and N400 old/new effects have also been reported in the test phase of another associative recognition paradigm in which items were either semantically related or unrelated word-pairs (Greve et al., 2007). Critically, the effects reported in that experiment could also be dissociated from one another; whereas the midfrontal old/new effect was sensitive to the semantic manipulation at study, the N400 old/new effect showed no difference between related and unrelated word pairs. This functional dissociation complements the electrophysiological dissociation reported in the current experiment to converge on the view that the N400 and the FN400 old/new effect reflect the combined engagement of distinct neuronal sources.

The current design, in which semantic priming was coupled with an incidental encoding phase, allowed for an efficient and participant-friendly approach to investigating the issue at hand. Nonetheless, it precluded counterbalancing of task order, allowing for the possibility that this could have caused the difference in distribution of the two effects. It is difficult to straightforwardly argue, however, how the presence of a preceding priming task would affect the distribution of a subsequently occurring effect. In line with this is the absence of evidence that N400 effects change qualitatively across different kinds of semantic processing tasks, even when the order of tasks is kept constant (Kutas, 1993). The lack of such indicators makes it unlikely that the effect observed in the second task of the current experiment is a frontally-shifted N400 which comes about because of an antecedent semantic processing task. Another potential limitation of the current design was the absence of process-pure measures of recognition processes, such as remember/know, confidence or associated source judgments. Without such measures it is not possible to unambiguously determine whether recognition judgments were made on the basis of familiarity and/or recollection. Such behavioral measures play an important role in the weight of evidence relating the early and late ERP old/new effects to familiarity and recollection, respectively (e.g. Vilberg et al., 2006; Woodruff et al., 2006), but have no direct bearing on the principal concern of the current study: determining whether there is a dissociation between two early aspects of the electrical record, the FN400 and N400, depending upon the tasks engaged.

In conclusion, when recorded in an episodic recognition task not confounded by manipulations of semantic priming, the FN400 index of correctly discriminating old and new items was electrophysiologically distinct from the N400, which was sensitive to the extent to which items had been semantically primed by the preceding item. This pattern serves to consolidate the role of the midfrontal old/new effect as a marker of episodic recognition and the necessary inferences in favor of dual-process models of recognition memory that have followed. The current data also point to the dangers that can arise from failing to employ appropriate operational definitions for critical ERP contrasts.

Acknowledgments

We thank Jérôme Rimpel and Marie Schwartz for the assistance with the stimuli preparation and data collection. This research was supported by the German Research Foundation under grant DFG-IRTG-1457 and was conducted in the International Research Training Group "Adaptive Minds" hosted by Saarland University, Saarbrücken (Germany).

References

- Aly, M., Yonelinas, A.P., Kishiyama, M.M., Knight, R.T., 2011. Damage to the lateral prefrontal cortex impairs familiarity but not recollection. *Behav. Brain Res.* 225, 297–304.
- Baayen, H., Piepenbrock, R., van Rijn, H., 1993. The CELEX Lexical Database. University of Pennsylvania, Linguistic Data Consortium.
- Bader, R., Mecklinger, A., Hoppstädter, M., Meyer, P., 2010. Recognition memory for one-trial-unitized word pairs: evidence from event-related potentials. *NeuroImage* 50 (2), 772–781.
- Bowles, B., Crupi, C., Mirsattari, S.M., Pigott, S.E., Parrent, A.G., Pruessner, J.C., Yonelinas, A.P., et al., 2007. Impaired familiarity with preserved recollection after anterior temporal-lobe resection that spares the hippocampus. *Proc. Natl. Acad. Sci.* 104, 16382–16387.
- Brown, M.W., Aggleton, J.P., 2001. Recognition memory: what are the roles of perirhinal cortex and hippocampus? *Nat. Rev. Neurosci.* 2, 51–61.
- Curran, T., 1999. The electrophysiology of incidental and intentional retrieval: ERP old/new effects in lexical decision and recognition memory. *Neuropsychologia* 37 (7), 771–785.
- Curran, T., 2000. Brain potentials of recollection and familiarity. *Mem. Cognit.* 28, 923–938.
- Curran, T., Cleary, A.M., 2003. Using ERPs to dissociate recollection from familiarity in picture recognition. *Cogn. Brain Res.* 15 (2), 191–205.
- Curran, T., Doyle, J., 2011. Picture superiority doubly dissociates the ERP correlates of recollection and familiarity. *J. Cogn. Neurosci.* 23 (5), 1247–1262.
- Dien, J., Santuzzi, A.M., 2005. Application of repeated measures ANOVA to high-density ERP datasets: a review and tutorial. In: Handy, T.C. (Ed.), *Event-Related Potentials: A Methods Handbook*. MIT Press, Cambridge, Massachusetts, pp. 1–73.
- Donaldson, D.I., Curran, T., 2007. Potential (ERP) studies of recognition memory for faces. *NeuroImage* 36 (2), 488–489.
- Ecker, U.K.H., Zimmer, H.D., 2009. ERP evidence for flexible adjustment of retrieval orientation and its influence on familiarity. *J. Cogn. Neurosci.* 21 (10), 1907–1919.
- Ecker, U.K.H., Zimmer, H.D., Groh-Bordin, C., 2007. Color and context: an ERP study on intrinsic and extrinsic feature binding in episodic memory. *Mem. Cognit.* 35, 1483–1501.
- Gardiner, J.M., 1988. Functional aspects of recollective experience. *Mem. Cognit.* 16, 309–313.
- Gratton, G., Coles, M.G.H., Donchin, E., 1983. A new method for off-line removal of ocular artifact. *Electroencephalogr. Clin. Neurophysiol.* 55, 468–484.
- Greve, A., van Rossum, M.C.W., Donaldson, D.I., 2007. Investigating the functional interaction between semantic and episodic memory: convergent behavioral and electrophysiological evidence for the role of familiarity. *NeuroImage* 34, 801–814.
- Groh-Bordin, C., Zimmer, H.D., Mecklinger, A., 2005. Feature binding in perceptual priming and in episodic object recognition: evidence from event-related brain potentials. *Cognitive Brain Research* 24 (3), 556–567.
- Groh-Bordin, C., Zimmer, H.D., Ecker, U.K.H., 2006. Has the butcher on the bus dyed his hair? When color changes modulate ERP correlates of familiarity and recollection. *NeuroImage* 32, 1879–1890.
- Grove, K.L., Wilding, E.L., 2009. Retrieval processes supporting judgments of recency. *J. Cogn. Neurosci.* 21 (3), 461–473.
- Henson, R.N., Cansino, S., Herron, J.E., Robb, W.G.K., Rugg, M.D., 2003. A familiarity signal in human anterior medial temporal cortex? *Hippocampus* 13 (2), 301–304.
- Holm, S., 1979. A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* 6, 65–70.
- Jäger, T., Mecklinger, A., Kipp, K.H., 2006. Intra- and inter-item associations doubly dissociate the electrophysiological correlates of familiarity and recollection. *Neuron* 535–545.
- Jasper, H.A., 1958. The ten–twenty system of the International Federation. *Electroencephalogr. Clin. Neurophysiol.* 10, 371–375.
- Kiss, G.R., Armstrong, C., Milroy, R., Piper, J., 1973. An associative thesaurus of English and its computer analysis. In: Aitken, A.J., Bailey, R.W., Hamilton-Smith, N. (Eds.), *The Computer and Literary Studies*. University Press, Edinburgh.
- Kounios, J., Holcomb, P.J., 1994. Concreteness effects in semantic processing: ERP evidence supporting dual-coding theory. *J. Exp. Psychol. Learn. Mem. Cogn.* 20 (4), 804–823.
- Küper, K., Heil, M., 2010. Letter search and relatedness proportion: further electrophysiological evidence for the automaticity of semantic activation. *Neurosci. Lett.* 482, 26–30.
- Küper, K., Groh-Bordin, C., Zimmer, H.D., Ecker, U.K.H., 2012. Electrophysiological correlates of exemplar-specific processes in implicit and explicit memory. *Cogn. Affect. Behav. Neurosci.* 12 (1), 52–64.
- Kutas, M., 1993. In the company of other words: electrophysiological evidence for single-word and sentence context effects. *Lang. Cognit. Process.* 8 (4), 533–572.
- Kutas, M., Federmeier, K.D., 2010. Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annu. Rev. Psychol.* 62, 621–647.
- Kutas, M., Hillyard, S.A., 1980. Reading senseless sentences: brain potentials reflect semantic incongruity. *Science* 207, 203–205.
- Kutas, M., Hillyard, S.A., 1984. Brain potentials during reading reflect word expectancy and semantic association. *Nature* 307, 161–163.
- Kutas, M., Federmeier, K.D., 2000. Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences* 4 (12), 463–470.
- Lau, E.F., Phillips, C., Poeppel, D., 2008. A cortical network for semantics: (de)constructing the N400. *Nat. Rev. Neurosci.* 9 (12), 920–933.
- MacPherson, S.E., Bozzali, M., Cipolotti, L., Dolan, R.J., Rees, J.H., Shallice, T., 2008. Effect of frontal lobe lesions on the recollection and familiarity components of recognition memory. *Neuropsychologia* 46, 3124–3132.
- Mandler, G., 1980. Recognizing: the judgment of previous occurrence. *Psychol. Rev.* 87, 252–271.
- McCarthy, G., Wood, C., 1985. Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. *Electroencephalogr. Clin. Neurophysiol.* 62, 203–208.
- McCarthy, G., Nobre, A.C., Bentin, S., Spencer, D.D., 1995. Language-related field potentials in the anterior-medial temporal lobe: I. Intracranial distribution and neural generators. *J. Neurosci.* 15 (2), 1080–1089.
- McElree, B., Dolan, P.O., Jacoby, L.L., 1999. Isolating the contributions of familiarity and source information to item recognition: a time course analysis. *J. Exp. Psychol. Learn. Mem. Cogn.* 25 (3), 563–582.
- Melinger, A., Weber, A., 2006. Database of Noun Associations for German. <http://www.coli.uni-saarland.de/projects/nag/>.
- Meyer, P., Mecklinger, A., Grunwald, T., Fell, J., Elger, C.E., Friederici, A.D., 2005. Language processing within the human medial temporal lobe. *Hippocampus* 15, 451–459.
- Meyer, P., Mecklinger, A., Friederici, A.D., 2010. On the processing of semantic aspects of experience in the anterior medial temporal lobe: an event-related fMRI study. *J. Cogn. Neurosci.* 22 (3), 590–601.
- Neely, J.H., 1977. Semantic priming and retrieval from lexical memory: roles of inhibitionless spreading activation and limited-capacity attention. *J. Exp. Psychol. Gen.* 106 (3), 226–254.
- Nessler, D., Mecklinger, A., Penney, T.B., 2001. Event-related brain potentials and illusory memories: the effects of differential encoding. *Cogn. Brain Res.* 10, 283–301.
- Nobre, A.C., McCarthy, G., 1995. Language-related field potentials in the anterior-medial temporal lobe: II. Effects of word type and semantic priming. *J. Neurosci.* 15, 1090–1098.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9 (1), 97–113.
- Paller, K.A., Voss, J.L., Boehm, S.G., 2007. Validating neural correlates of familiarity. *Trends Cogn. Sci.* 11 (6), 243–250.
- Picton, T.W., Bentin, S., Berg, P., Donchin, E., Hillyard, S.A., Johnson, R., Miller, G.A., et al., 2000. Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiology* 37 (2), 127–152.
- Raaijmakers, J., Schrijnemakers, J.M.C., Gremmen, F., 1999. How to deal with “the language-as-fixed-effect fallacy”: common misconceptions and alternative solutions. *J. Mem. Lang.* 41 (3), 416–426.
- Rossell, S.L., Price, C.J., Nobre, A.C., 2003. The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia* 41 (5), 550–564.
- Rugg, M.D., Coles, M.G.H., 1995. The ERP and cognitive psychology: conceptual issues. In: Rugg, M.D., Coles, M.G.H. (Eds.), *Electrophysiology of Mind: Event-Related Brain Potentials and Cognition*. Oxford University Press, Oxford, pp. 27–39.
- Rugg, M.D., Curran, T., 2007. Event-related potentials and recognition memory. *Trends Cogn. Sci.* 11, 251–257.
- Sauvage, M.M., Beer, Z., Eichenbaum, H., 2010. Recognition memory: adding a response deadline eliminates recollection but spares familiarity. *Learn. Mem.* 17 (2), 104–108.
- Schloerscheidt, A.M., Rugg, M.D., 2004. The impact of change in stimulus format on the electrophysiological indices of recognition. *Neuropsychologia* 42, 451–466.
- Skinner, E.I., Fernandes, M.A., 2007. Neural correlates of recollection and familiarity: a review of neuroimaging and patient data. *Neuropsychologia* 45 (10), 2163–2179.
- Snodgrass, J.G., Corwin, J., 1988. Pragmatics of measuring recognition memory: applications to dementia and amnesia. *J. Exp. Psychol. Gen.* 117, 34–50.
- Stenberg, G., Hellman, J., Johansson, M., Rosen, I., 2009. Familiarity or conceptual priming: event-related potentials in name recognition. *J. Cogn. Neurosci.* 21 (3), 447–460.
- Unsworth, N., Heitz, R.P., Schrock, J.C., Engle, R.W., 2005. An automated version of the operation span task. *Behav. Res. Methods* 37, 498–505.
- Urbach, T.P., Kutas, M., 2006. Interpreting event-related brain potential (ERP) distributions: implications of baseline potentials and variability with application to amplitude normalization by vector scaling. *Biol. Psychol.* 72 (3), 333–343.
- Vilberg, K.L., Rugg, M.D., 2009. Functional significance of retrieval-related activity in lateral parietal cortex: evidence from fMRI and ERPs. *Hum. Brain Mapp.* 30 (5), 1490–1501.
- Vilberg, K.L., Moosavi, R.F., Rugg, M.D., 2006. The relationship between electrophysiological correlates of recollection and amount of information retrieved. *Brain Res.* 1122, 161–170.
- Voss, J.L., Federmeier, K.D., 2011. FN400 potentials are functionally identical to N400 potentials and reflect semantic processing during recognition testing. *Psychophysiology* 48 (4), 532–546.
- Voss, J.L., Gonsalves, B.D., 2010. Time to go our separate ways: opposite effects of study duration on priming and recognition reveal distinct neural substrates. *Front. Hum. Neurosci.* 4, 227–237.
- Voss, J.L., Paller, K.A., 2007. Neural correlates of conceptual implicit memory and their contamination of putative neural correlates of explicit memory. *Learn. Mem.* 14 (4), 259–267.
- Voss, J.L., Lucas, H.D., Paller, K.A., 2010. Conceptual priming and familiarity: different expressions of memory during recognition testing with distinct neurophysiological correlates. *J. Cogn. Neurosci.* 22 (11), 2638–2651.

- Wagner, A.D., Gabrieli, J.D., 1998. On the relationship between recognition familiarity and perceptual fluency: evidence for distinct mnemonic processes. *Acta Psychol.* 98 (2–3), 211–230.
- Wang, W.-C., Lazzara, M.M., Ranganath, C., Knight, R.T., Yonelinas, A.P., 2010. The medial temporal lobe supports conceptual implicit memory. *Neuron* 68 (5), 835–842.
- Wiegand, I., Bader, R., Mecklinger, A., 2010. Multiple ways to the prior occurrence of an event: an electrophysiological dissociation of experimental and conceptually driven familiarity in recognition memory. *Brain Res.* 1360, 106–118.
- Wilding, E.L., 2000. In what way does the parietal ERP old/new effect index recollection? *Int. J. Psychophysiol.* 35 (1), 81–87.
- Wilding, E.L., 2006. The practice of rescaling scalp-recorded event-related potentials. *Biol. Psychol.* 72, 325–332.
- Wilding, E.L., Herron, J.E., 2006. Electrophysiological measures of episodic memory control and memory retrieval. *Clin. EEG Neurosci.* 37 (4), 315–321.
- Wilding, E.L., Rugg, M.D., 1996. An event-related potential study of recognition memory with and without retrieval of source. *Neuropsychologia* 37, 441–454.
- Wilding, E.L., Doyle, M.C., Rugg, M.D., 1995. Recognition memory with and without retrieval of context: an event-related potential study. *Neuropsychologia* 33, 743–767.
- Woodruff, C.C., Hayama, H.R., Rugg, M.D., 2006. Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Brain Res.* 1100, 125–135.
- Yonelinas, A.P., 2002. The nature of recollection and familiarity: a review of 30 years of research. *J. Mem. Lang.* 46, 441–517.
- 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. *J. Neurosci.* 25, 3002–3008.
- Yonelinas, A.P., Aly, M., Wang, W.-C., Koen, J.D., 2010. Recollection and familiarity: examining controversial assumptions and new directions. *Hippocampus* 20, 1178–1194.
- Yovel, G., Paller, K.A., 2004. The neural basis of the butcher-on-the-bus phenomenon: when a face seems familiar but is not remembered. *NeuroImage* 21, 789–800.
- Yu, S.S., Rugg, M.D., 2010. Dissociation of the electrophysiological correlates of familiarity strength and item repetition. *Brain Res.* 1320, 74–84.