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Electrophysiological Measures of Familiarity Memory

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Key Words

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ABSTRACT

Event-related potentials are a valuable tool for the study of human memory function. This selective review provides a brief introduction in models of recognition memory and then describes how ERPs can be used to investigate familiarity memory, an acontextual form of remembering that can be distinguished from the recollection of detailed information of prior events. ERP studies on the mid-frontal old/new effect, the putative electrophysiological correlate of familiarity memory are reviewed. It will be illustrated how familiarity memory is reflected in this effect, how it can electrophysiologically be dissociated from other forms of memory and which brain systems mediate this form of remembering. Recent studies will be reviewed that illustrate that familiarity is not only restricted to single items but can also support the retrieval of associative information.

INTRODUCTION

We all know the sometimes embarrassing experience of meeting someone, who is familiar to us without being able to remember any specific details about that person like his/her name or any prior encounters with him/her. This indicates that in some situations, our memory can completely rely on feelings of familiarity, whereas in other contexts we can recall specific details about prior episodes. Common to contemporary models of human memory is the view that a stimulus presented in a context resonates with a memory trace and causes the generation of mental contexts.[1,2] The strength of that generation dictates the subject's reaction to it, be it a feeling of familiarity or a recollective experience. Accordingly, dual process models of recognition memory propose that recognition memory can be based on two processes, a relatively slow recall-like process that retrieves detailed memories about prior episodes (recollection) and a fast operating global matching process that entails acontextual memories (familiarity) and does not support the retrieval of contextual information that is characteristic for recollection.[3]

Even though dual process models assume that recognition memory judgments can be based on two distinct forms of memory, they differ in important ways and make conflicting predictions on the functional characteristics and neuronal correlates of the two memory systems. For example, some models assume that familiarity can be equated with processing fluency, a mechanism that also supports implicit memory.[4] Other models propose that familiarity reflects a more perceptual or sensory process, whereas recollection is assumed to be an elaborative or conceptual process.[5] Tulving and colleagues[6,7] assume a relationship of redundancy between familiarity and recollection. Though not frequently described as a dual process model, Tulving proposes an episodic memory system that gives rise to the (conscious) experience of remembering (recollection). The episodic memory system is embedded and partly independent from a semantic memory system that gives rise to the experience of knowing (i.e., familiarity with facts and events of the real world) Yonelinas[8] assumes that familiarity reflects the assessment of quantitative memory strength, whereas recollection is more like a threshold retrieval process by which qualitative information about a prior episode is retrieved. Items that fall below a recognition threshold are retrieved on the basis of familiarity, whereas for those events for which accurate information can be retrieved, recollection is expected.

A recent dual process model which was developed on the basis of neuroanatomical and neurophysiological properties of the medial temporal lobes (MTL)[2] assumes that recollection-based memory critically depends on the hippocampus, a brain structure that allows to encode distinct (pattern separated) representations of episodes that facilitate pattern completion (i.e., recollection) at retrieval. In contrast, MTL structures surrounding the hippocampus, i.e., the perirhinal and entorhinal cortices are involved in familiarity discrimination. These MTL structures are polymodal association cortices. They assign similar activation

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patterns to similar inputs and are capable of extracting the shared structure of events (i.e, sharpening).The latter system does not support recall but it supports familiarity for the information it represents. The Norman and O'Reilly[2] model can adequately simulate a large variety of recognition memory phenomena and is also supported by recent neuropsychological and neuroimaging studies that show that the hippocampus and adjacent MTL structures independently contribute to familiarity and recollection.[9-12]

Event-related potentials and recognition memory

While a variety of behavioral techniques have been developed to measure familiarity and recollection (for an overview see Yonelinas,[8] in recent years ERPs have been more and more used in experimental memory research to study the distinction between familiarity and recollection. The relevant data comes from the analyses of ERP old/new effects (or episodic memory effects), i.e., the differences in the ERP waveforms elicited by correctly rejected new (unstudied) items and correctly classified old (studied) items in recognition memory tasks. The logic behind this comparison is that for items correctly classified as "new" any interaction between a retrieval cue and a memory trace can be excluded. By this, differences in the ERP waveforms elicited by old and new items can be taken as a correlate of successful memory retrieval. Early ERP studies on recognition memory have revealed a parietally distributed old/new effect (often called the parietal old/new effect), that took the form of more positive going ERP waveforms for old than for new items in the time interval from 400 to 800 ms after onset of the retrieval cue.[13,14] Due to the invention of high-density EEG recording techniques and more sophisticated experimental techniques and manipulations, it is a well established fact that there is an ensemble of ERP old/new effects that can be dissociated on the basis of their topographical distribution across the scalp, their time course and their sensitivity to experimental manipulations.[15,16] The presence of a variety of ERP old/new effects that are associated with different aspects of memory retrieval not only makes the ERP technique a valuable tool to examine models of human memory functions.[17] ERP old/new effects are also suitable for studying memory dysfunctions and their recovery after brain damage.[18,19]

The mid-frontal old/new effect

In the following I will focus on one ERP effect, the mid-frontal old/new effect that has been associated with familiarity-based recognition judgments. For an overview of ERP recognition memory effects see Friedman and Johnson.[15] A comprehensive review of the parietal old/new effect can be found in the article by Wilding and Herron in this issue. Different approaches have been used to study the contribution of familiarity to ERPs in recognition memory tasks. One approach has been to manipulate the general similarity between information from a previous study phase and the test items. Those studies found that the similarity between study and test information modulates the ERP old/new effect at frontal recording sites in a systematic way.

Curran[20] used the so-called plurality recognition task, in which words from a previous study phase (HOUSE) at test were presented together with plurality reversed words (HOUSES) and new words (TABLE). Correctly identified old words and plurality reversed words erroneously classified as old elicited more positive going ERP waveforms between 300 and 500 ms at frontal recording sites relative to new words. Similar results have been reported for mirror-reversed pictures,[21] and geometrically similar shapes.[22] On the basis of its resemblance to the N400 component in language studies[23] and its topographical maximum at frontal recording sites, this effect has been called the FN400 effect by Curran and colleagues. In the following the term mid-frontal old/new effect will be used to refer to the more positive going waveforms for repeated as compared to new items between 300 and 500 ms, being most pronounced at frontal and fronto-central recording sites.

On the basis of its sensitivity to the overall similarity between study and test information the mid-frontal old/new effect has been taken as an electrophysiological correlate of familiarity-based recognition, with the assumption being that familiarity arises from a global matching process between the features of a stimulus and the contents of a memory trace. The observation that the mid-frontal old/new effect is also observed for meaningless geometrical shapes[22,24] or unfamiliar faces[25] argues against the recently proposed view that this effect should be considered as an electrophysiological correlate of conceptual priming.[26]

Mecklinger and colleagues[16,27] provided further evidence for the view that the mid-frontal old/new effect is associated with familiarity arising from the global similarity between study and test items. Using a false memory paradigm with an auditory study phase and a visual test phase in which studied words had to be discriminated from words of the same semantic category and from new words, we found the same mid-frontal old/new effect for old words and false responses to semantically related (lure) words. The observation that the mid-frontal old/new effect to semantically related (lure) words declines when the retention interval is increased, whereas ERP indices of recollection were not affected by this manipulation[28] supports models of recognition memory that assume that familiarity decreases more rapidly than recollection.[8] Notably, as the aforementioned studies used a cross-modal study test procedure (Study: auditory / Test: visual) they also indicate that the global matching process reflected in the mid-frontal old/new effect is not restricted to a purely perceptual level, but can also operate on an amodal, conceptual-semantic level. That is, depending on information provided by a retrieval cue and the information stored in long-term memory, perceptual or higher order conceptual stimulus attributes (e.g., object names) can enter the cue-trace matching process.

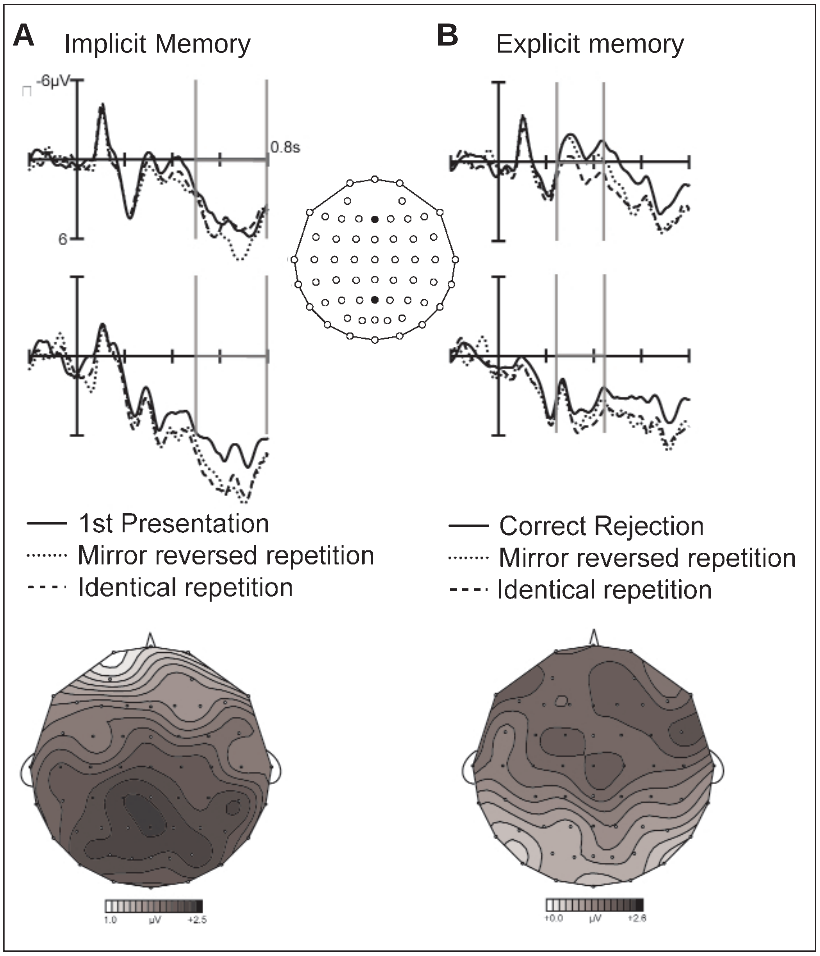

Figure 1. (A) Grand average ERPs to new stimuli, identical and mirror-reversed repetitions of the stimuli in the implicit memory task of the Groh-Bordin et al[29] study at a frontal and a parietal recording site. The maps show the difference between the scalp topography of the new stimuli and the old stimuli, collapsed across congruent and incongruent repetitions. The maps were computed for the 500 to 800 ms interval after stimulus onset, in which the implicit memory effect was largest. (B) Grand average ERPs to new stimuli, identical and mirror-reversed repetitions of the stimuli at a frontal and a parietal recording site in the explicit memory task. The maps show the difference between the scalp topography of the new stimuli and the old congruent stimuli in the 250 to 450 ms time interval in which the mid-frontal old/new effect was largest. Dark grey areas denote topographical regions with large positive voltages differences between first and second presentations. The time windows used for statistical analyses are denoted by the two vertical grey lines in the ERP diagrams. This is a modified version of a figure presented by Groh-Bordin, Zimmer, Mecklinger.[31]

Familiarity memory and implicit memory

While a variety of studies has shown that the mid-frontal old/new effect can be functionally dissociated from the parietal old/new effect (the putative correlate of recollection), establishing this effect as an electrophysiological correlate of familiarity-based recognition presupposes that it can also be dissociated from other ERP manifestations of memory processes. An important issue is whether familiarity-based recognition and behavioral facilitation (priming) can electrophysiologically be dissociated. If a common mechanism underlies familiarity-based recognition and priming in implicit memory tests as proposed by some dual process models[4] both processes should be associated with qualitatively identical ERP effects. Conversely, if the two processes are independent, it should be possible to show a double dissociation, i.e., to find variables that have an effect on one process and not the other and vice versa. In support of the independence view, Groh-Bordin, Zimmer and Mecklinger[29] showed that familiarity and priming can electrophysiologically be dissociated. Participants performed an implict task (living / non-living decisions) and an explicit recognition memory task with figural stimuli. In the implicit task a similar amount of priming was obtained for identical repetitions and mirror-reversed repetitions of the stimuli and both second presentations elicited a broadly distributed positive slow wave with a parieto-occipial maximum between 500 and 800 ms (see Figure 1A). In contrast, in the explicit test, identical repetitions but not mirror-reversed repetitions elicited a frontal old/new effect between 250 and 450 ms, resembling the mid-frontal old/new effect, the putative correlate of familiarity-based recognition (see Figure 1B). To account for this electrophysiological dissociation it is proposed that familiarity can be used for memory decisions only when a retrieval mode is adapted. Retrieval mode refers to a brain state that ensures that a stimulus is treated as cue for the retrieval of episodic memory.[29,30] The

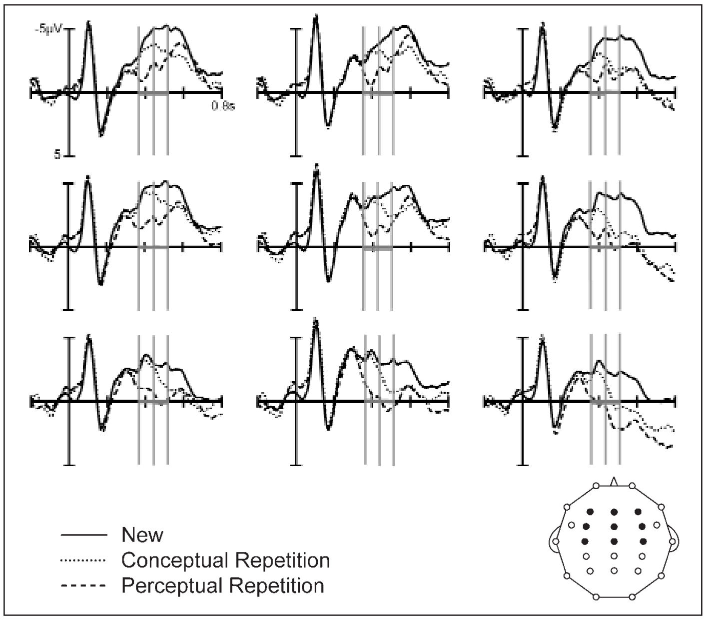

Figure 2.
Grand average ERPs for 17 participants elicited by visually presented new objects and objects that were presented as object or as spoken words in the study phase. The ERPs are shown for 9 electrodes at left, middle and right frontal and central recording sites. For details see legend of Figure 1. The two time windows used for the statistical analyses of the early (350 to 450 ms) and the mid-frontal old/new effect (450 to 550 ms) are denoted by the three vertical grey lines.

adaptation of such a retrieval mode in an explicit memory task may ensure that particular kinds of episodic information can be retrieved upon presentation of a cue. By this, it makes information available that is not accessible in implicit test (see Groh et al[29] for further details).

Similar dissociations between the ERP correlates of perceptual fluency in implicit memory test and ERP indices of explicit memory have been reported in a variety of studies with visual stimulus materials.[32-35] The posterior distributed ERP slow waves may reflect the activation of repetition sensitive higher order visual processing areas.[36]

Conceptual vs perceptual similarity

Another important issue in establishing the functional significance of the mid-frontal old/new effect is to determine how the mid-frontal effect is related to changes in the similarity between study and test stimuli. Is the mid-frontal old/new effect sensitive to study-test similarity in a graded manner or does it reflect the presence or absence of similarity in an all-or-none manner? The empirical evidence on this issue is mixed: A recent study by Curran and Dien,[37] (in the following referred to as C&D) for example revealed that familiarity is an amodal process that shows no sensitivity to perceptual variables at all. The study manipulated the study modality (visual / auditory) of visually tested words. The mid-frontal old/new effect (300 to 500 ms) was not affected by study modality, i.e., it was statistically not different for within-modality and across-modality repetitions. An earlier old/new effect between 180-260 ms with a frontopolar distribution was obtained for visually studied words, only. Notably, the aforementioned mid-frontal effect between 300 and 500 ms tended to be larger for visually studied words than for auditory studied words. However, as this effect did not reach the significance level, the C&D data suggest that familiarity is an amodel process in which conceptual/semantic attributes play a major role and perceptual variables are of minor relevance.

Conversely, in a recent study using line drawings of real world objects as stimulus materials, we found the mid-frontal old/new effect to be sensitive to study-test similarity (Mecklinger, Brinkmann, Czernochowski, Zink, unpublished). As in the C&D experiment, study modality (spoken words / objects) was manipulated and recognition memory was tested for visually presented objects. This allows to examine the effects of perceptual (studied objects) and conceptual repetition (studied words) on the mid frontal old/new effect. Three results were obtained (cf. Figure 2): First, as in the C&D study an early effect between 350 and 450 ms that preceded the mid-frontal old/new effect was obtained for perceptual but not for conceptual repetitions. Second, there was a mid-frontal old/new effect between 450 to 550 ms for both, perceptual and conceptual repetitions. Third, while the latter effect was of similar magnitude for both kinds of repetitions at frontal and fronto-central recordings, it was larger for perceptual than for conceptual repetitions at central recording sites. This indicates that even though conceptual representations are sufficient for the cue-trace matching process, the similarity of study and test features in the perceptual repetition condition in our study has additionally contributed to familiarity memory. To reconcile the different results of our study and the C&D study it is important to keep in mind that perceptual repetition was examined with visually rich line drawings of real world objects in our study and with written words in the C&D study. Given this, it is reasonable to assume that under task situations in which visu-

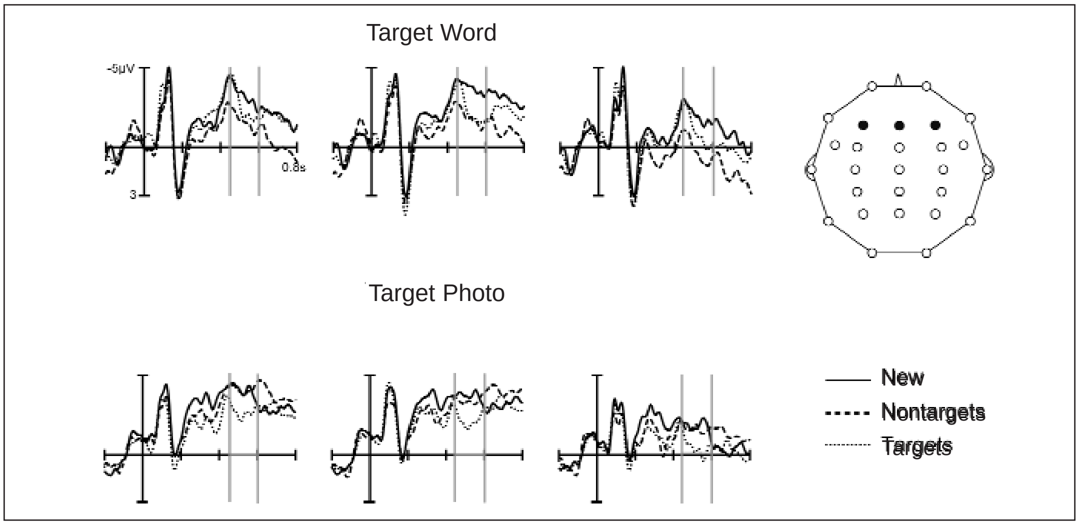

Figure 3.
Grand average ERPs evoked by correct judgments to targets, nontargets and new items in the study by Czernochowski et al.[38] The data is illustrated for left, middle and right frontal recording sites for the Target Word condition (perceptual matching of nontargets) in the upper row and the Target Photo (conceptual matching of nontargets) in the lower row. In both conditions, the test stimuli were line drawings of objects. The figure is based on the data presented in the study of Czernochowski et al.[38] For details see legend of Figure 1.

ally detailed information is available at study and test, matching of study-test features on the perceptual level can enhance the conceptual matching process and additionally contributes to familiarity memory.

Further insights in the contribution of perceptual and conceptual features for the global matching processes underlying familiarity memory comes from a recent ERP study on recognition memory in children and adults.[38] In a memory exclusion task[4] participants studied spoken words and photographs denoting real world objects in different blocks. In the test phase line drawings of the studied objects of both blocks were presented together with new objects. The participants had to respond “old” when the line drawing denotes an object of one study context (targets) and “new” items from the other study context and for completely new stimuli. Of special interest were the adults’ ERP waveforms evoked by nontarget stimuli, i.e., stimuli that had to be rejected as new even though they had been studied before. On the basis of a global-matching account of familiarity memory we assumed that nontargets due to their status as “studied materials” should evoke familiarity memory even though they had to be classified as “new.” In fact, nontargets elicited a mid-frontal old/new effect between 200 and 400 ms that was nondistinguishable from the effect obtained for target stimuli.

The version of the memory exclusion task employed in the Czernochowski et al[38] study allows to further fractionate the nontarget old/new effect according to the level of cue-trace matching. Global matching for nontargets was restricted to the conceptual level when studied words had to be rejected as new (e.g., participants heard the word “house” at study and had to press the “new” button when a line drawing of a house was presented at test). Conversely, visual attributes were available for the nontarget matching process when studied photographs had to be rejected (e.g. ,participants saw a photograph of a “car” at study and subsequently had to classify a line drawing of the car as new). The ERP waveforms elicited by nontarget photos (perceptual matching) and nontarget words (conceptual matching) are illustrated in the upper and lower row of Figure 3, respectively. Notably in the perceptual matching condition the nontarget old-new effect at frontal sites in the 450 to 650 ms time period was statistically identical to the target old/new effect, whereas in the conceptual matching condition (studied words as nontargets) no mid-frontal effect in this time period was observed. The latter effects were delayed relative to the nontarget old/new effects collapsed across both study modalities, for reasons that have to be determined. Nevertheless, these results underscore the high relevance of the visual similarity between study and test features for familiarity memory. For visually rich stimuli, cue-trace matching seems to rely more on perceptual features, whereas for words as stimulus materials and/or generally low study-test feature overlap (as in cross-modal task designs) higher order conceptual features play a greater role for familiarity memory.

Important issues to be investigated in further studies are (i) whether conceptual and perceptually based matching are mediated by overlapping but qualitatively different brain systems and (ii) the processing mechanism reflected by the early old/new effects starting around 250 ms after stimulus onset (see Curran and Dien[37] for an explanation). Further research using parametrical manipulations of study-test similarity may elucidate the joint contribution of perceptual and conceptual feature match on familiarity memory.

Familiarity and associative information

A final issue to be addressed here is whether familiarity memory is item-specific or also occurs for associative information. As outlined above, most dual process models assume that familiarity reflects a purely quantitative (strength-like) memory signal that supports recognition of single items, whereas recollection supports the retrieval of qualitative and associative information about items and their study context. This view would imply that cue-trace matching as reflected in familiarity memory operates on the item level and cannot take associations of items into account. By this, familiarity should not be sensitive to whether items occurred together at study and should not contribute to associative recognition. However, recent studies suggest that this view is too simplistic. They showed that familiarity can support associative recognition in situations in which the to-be-associated information can be unitized to a single and larger representation. This phenomenon can be illustrated by a recent face recognition memory study by Yonelinas, Kroll, Dobbins and Soltani.[39] They examined associative recognition for faces that had to be discriminated from distractor faces. The distractor faces were composed of parts of the study faces and all faces were presented either upright (allowing to treat the face as a whole item) or upside down at study and test. Notably, significant behavioral estimates of familiarity were obtained only when the faces were presented upright. This suggests that familiarity may support associative recognition in situations that foster the encoding of associative representations as the unitisation of face parts to a global face representation.

We set out to examine whether associative effects on familiarity are also obtained with other stimulus materials and testing conditions. In addition, rather than using behavioral estimates of familiarity, the mid-frontal old/new effect was used as a correlate of familiarity memory.[40] We examined associative recognition of two forms of feature conjunctions: Namely, feature conjunctions that can be easily encoded as a single unitized representation, and feature conjunctions for which unitisation is difficult to accomplish. Emotion words that were spoken in an emotionally congruent prosody (the word “killed” spoken in an angry prosody) or in a neutral prosody served as stimulus materials. The prediction was that words spoken in congruent prosody can be encoded and memorized as single, unitized representations (e.g., “something negative”) that allow cue-trace matching on the level of unitized representations and recognition supported by familiarity. For words spoken in neutral prosody the semantic and prosodic features are hard to unitize and as a consequence recognition should not be supported by familiarity. A cross-modal source memory task was used in which study words were presented auditorily followed by visual test words. To foster the processing of word-prosody associations, each old/new judgment for the emotion words was followed by a source judgment by which the participants indicated whether the word was spoken in congruent or neutral prosody at study.

Source memory performance was much better for women than for men (74 % vs. 64% correct judgments), indicating that women were more efficient in integrating verbally and prosodically expressed emotions. Only the ERP waveforms elicited by new words, old congruent and neutral words collapsed across positive and negative valence of the words for female participants (n=16) are presented here, as they are of most relevance for associative recognition. Consistent with the view, that congruent word-prosody pairings can easily be encoded as unitized representations and allow familiarity memory to occur, there was a reliable old/new effect between 250 and 450 ms with a fronto-central maximum for words spoken in congruent prosody (cf Figure 4). No such effects were obtained for neutral words.

Prior to discussing the latter effect in the light of associative effects on familiarity, some objections have to be taken into account. First, the mid-frontal effect was only present for women. This may suggest that the sensitivity of familiarity to associative recognition depends on the efficiency with which these associations are encoded and maintained (at least for emotional stimuli). Second, the contrast between the congruent and neutral prosody of a word may have been too weak to foster unitization for all congruent pairings to a similar extend. Despite these objections, the aforementioned results indicate that associative recognition by no means is restricted to recollection. They rather suggest that cue-trace matching can operate on associations of features and that familiarity can support associative recognition in situations in which the to-be-associated features, or items can be unitized to form a coherent higher order representation.

In providing preliminary evidence for the sensitivity of familiarity memory to feature conjunctions the present results are also consistent with neuroanatomically constraint models of recognition memory.[2,41,42] Familiarity may benefit from lower-order associations between features that are formed by those MTL structures that are directly involved in representing the stimulus features (see also[43]). In fact, experimental lesion studies in monkeys showed that neurons in the perirhinal cortex respond maximally to both members of particular paired stimuli (i.e., pair coding) and by this are capable of associative coding.[44] Conversely, it is well established in a large variety of models on hippocampal functioning that a key processing mechanism of the hippocampus is the encoding and storage of arbitrary feature conjunctions.[2,41,45] These conjunc-

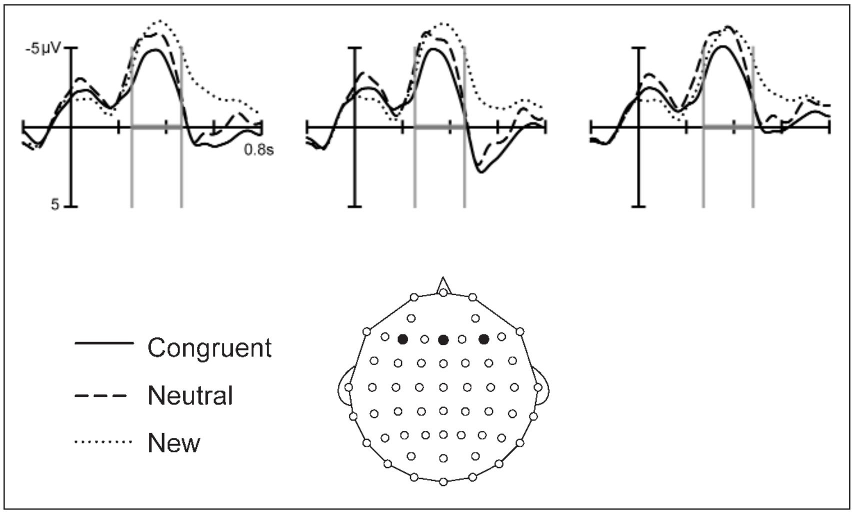

Figure 4.
Grand average ERP waveforms evoked by correctly classified new emotion words and words spoken in congruent or neutral prosody at study. Only the data of female participants is illustrated for left, middle and right frontal recording sites. The x-axis depicts the time interval from 200 ms before onset of the test words until 1000 ms thereafter. For details see legend of Figure 1.

tive representations of the hippocampus make it well suited for associative recognition and other forms of episodic memory requiring the retrieval of item context conjunctions and may account for its superior role in associative memory as compared to adjacent MTL structures.

SUMMARY

This review gives a brief overview on dual process models of recognition memory. Recent ERP studies on recognition memory are reviewed that show the mid-frontal old/new effect in the ERP is sensitive to the overall similarity between study and test information. Under the assumption that familiarity arises from a global cue-trace matching process, the mid-frontal old/new effect can be taken as a correlate of familiarity memory. In a next step, the relevance of perceptual and conceptual stimulus attributes for the global matching process are reviewed. Finally, empirical evidence is provided for the view that familiarity does not only support recognition of single items but under some circumstances can also be sensitive to feature conjunctions and support associative recognition. These insights in how familiarity memory is reflected in the mid-frontal old/new effect should be taken as a starting point for future ERP studies on memory functions. They may stimulate new research not only on how our memory system can be cued by external information in order to retrieve the past but also on how these memory processes are degraded by brain lesions.

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