Episodic memory storage and retrieval: Insights from electrophysiological measures

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Introduction: Dual-process models of recognition memory

Recognition memory refers to the ability of becoming aware that a particular item or information has been encountered in a previous episode. The present chapter will deal with this form of episodic memory by considering theoretical assumptions about its basic cognitive mechanisms. Furthermore, it will be demonstrated how electrophysiological measures of human brain activity have promoted our understanding of the neurocognitive processes involved in recognition memory and by this have supported models of episodic memory.

A fundamental question in contemporary memory research is whether a single type of memory can account for recognition memory performance or whether recognition memory involves more than a single memory process. While the latter class of models (i.e. dual process models) emphasize on empirical dissociations that cannot be accounted for by the view that recognition memory involves just one type of memory, opponents of the former view argue that some dissociations can more simply be interpreted in terms of strong and weak memories (Squire, Wixted, & Clark 2007).

The core assumption of a variety of dual-process models is that recognizing can be based on two distinct phenomenal experiences: *Familiarity*-based recognition occurs when someone has a feeling of ‘knowing’ an item from somewhere, but cannot recall any further information on the episodic context during which the item was originally experienced. By contrast, if *recollection*-based recognition occurs, then such contextual information (e.g., the spatio-temporal context of the episode) can be retrieved. This distinction of familiarity and recollection as two basic and distinguishable sub-processes underlying our ability to recognize previously encountered information has been established in formal dual-process models of recognition memory (e.g., Aggleton & Brown, 1999, 2006; Jacoby, 1991; Mandler, 1980; Quamme, Yonelinas, & Kroll, 2006; Tulving, 1985; Yonelinas, 2001, 2002; but see Hirshman & Master, 1997; Slotnick & Dodson, 2005, for different views). To date, a considerable body of evidence has been obtained in the support of proposals of the dual-process account (see Aggleton & Brown, 2006; Yonelinas, 2002, for reviews).

The central characteristics of familiarity and recollection as described by formal dual-process models are the following (see Yonelinas, 2002): Familiarity is assumed to reflect a fast-acting, relatively automatic, and item-specific memory process. Some models propose that information supporting familiarity is of continuously varying strength, whereby the familiarity of ‘old’ (i.e., studied) and ‘new’ (i.e., unstudied) items form overlapping Gaussian distributions (Yonelinas, 1997). By contrast, recollection is considered a somewhat slower and more effortful/elaborate memory process that can establish links between arbitrary information (e.g., items and contextual information). Some models assume that information supporting recollection has a threshold-like character, resulting in the retrieval of items with high confidence if they exceed a certain threshold, or producing retrieval failures if items fall below the threshold above which recollection can occur.

After establishing the basic functional characteristics of familiarity and recollection, the question arises how the contributions of these two processes can be estimated in a recognition memory task at hand. Several techniques and operational definitions have been proposed to derive behavioral estimates of familiarity and recollection from observed parameters of performance through the application of model equations (see Quamme et al., 2006; Yonelinas, 2002, for reviews). The most important of these techniques involve the process-dissociation procedure (Jacoby, 1991), the remember/know procedure (Tulving, 1985), and the receiver operating characteristics (ROC) procedure (Yonelinas, 1997). It is worth noting that the derivation of estimates by using these techniques relies on specific model constraints, such as the assumption that familiarity and recollection operate independently (Rugg & Yonelinas, 2003).

Familiarity and recollection have been found to be distinguishable on a physiological basis, as they seem to rely on partially non-overlapping neuronal networks. The medial temporal lobe is essential for declarative long-term memory in general, but within this structure the hippocampal formation is assumed to play a significant role for recollection. In the surrounding parahippocampal region comprising the entorhinal, perirhinal, and parahippocampal cortices, the anterior part centered around the perirhinal cortex seems to be the generator of familiarity signals (Aggleton & Brown, 2006). In the following, the source of familiarity information will be referred to as anterior medial temporal lobe cortex (MTLC). A considerable number of neuroimaging and animal studies supports the hypothesis that familiarity and recollection critically rely on the hippocampus and anterior MTLC, respectively (e.g., Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Grill-Spector, Henson, & Martin, 2006; Henson, Cansino, Herron, Robb, & Rugg, 2003; Li, Miller, & Desimone, 1993; Montaldi, Spencer, Roberts, & Mayes, 2006). Recently, also lateral and medial prefrontal and parietal regions have been found to be differently activated by familiarity and recollection (Yonelinas, Otten, Shaw, & Rugg, 2005). Rather than reflecting functions that are specific for familiarity and recollection, these prefrontal and parietal regions may reflect processes supporting memory retrieval or processes that act downstream from the computation of familiarity and recollection signals, such as the monitoring or verification of retrieved information or the focusing of attention to retrieved information (Wagner, Shannon, Kahn, & Bucker, 2005).

Further support for the neuroanatomical dissociation of familiarity and recollection is provided by neuropsychological case studies, revealing that brain lesions including the hippocampus and surrounding MTLC disrupt both recollection and familiarity, whereas selective hippocampal damage appears to disrupt recollection while leaving familiarity relatively intact (e.g., Holdstock, Mayes, Gong, Roberts, & Kapur, 2005; Mayes, Holdstock, Isaac, Hunkin, & Roberts, 2002; Mecklinger, Cramon, & Matthes-von Cramon, 1998; Yonelinas et al., 2002; see Quamme et al., 2006, for a review). Conversely, recent neuropsychological case studies and animal studies found evidence for both recollection and familiarity signals in the hippocampus (Squire et al., 2007; Wais, Wixted, Hopkins, & Squire, 2006).

In an attempt to formalize and model the neurocognitive mechanisms underlying familiarity and recollection, Norman and O'Reilly (2003) have put forth an integrative neural-network model of recognition memory. In this intriguing model, the physiological properties of the hippocampus and surrounding anterior MTLC structures are taken as constraints for computational principles. The hippocampal formation with its sparse level of neural firing is proposed to be critical for recollection because it can establish associations between nonoverlapping, arbitrarily paired items that are themselves represented in anterior MTLC. Specifically, the hippocampus creates pattern-separated representations of to-be-associated items in region CA3 that are linked to each other and to a copy of the anterior MTLC input pattern via region CA1. At test, the hippocampus enables pattern-completion and retrieves the complete studied pattern in response to a partial cue. However, note that this recollection mechanism may break down when the overlap between to-be-associated information is too high, since pattern-separated representations cannot be established in this case (Schacter, Norman, & Koutstaal, 1998).

By contrast, consistent with findings of neuroimaging and animal studies, Norman and O'Reilly (2003) assume that familiarity judgments are supported by the anterior MTLC on the basis of the relative sharpness of item representations. During learning, a sharpening process results in a smaller number of anterior MTLC neurons that are specifically tuned to represent a particular stimulus whereas other neurons are inhibited, which decreases total anterior MTLC activity in response to a familiar relative to a novel item and enables familiarity-based recognition judgments (cf. Grill-Spector et al., 2006). Furthermore, the anterior MTLC is suggested to assign overlapping representations to similar stimuli, which enables the extraction of shared structures of items and statistical regularities of the environment. An important feature of the model is that the same anterior MTLC structures are involved in both extracting and representing stimulus features and computing familiarity signals.

In sum, considerable evidence from behavioral, neuroimaging, animal, and neuropsychological studies supports the distinction between familiarity and recollection as two basic and qualitatively distinct mechanisms underlying our ability to recognize previously encountered information. With regard to their neural substrates, recollection is assumed to critically rely on the functional integrity of the hippocampus, whereas familiarity seems to be generated independently by the adjacent cortical regions (i.e., anterior MTLC). Prefrontal and parietal regions that are frequently found to be activated in recognition memory tasks are presumably not specifically tied to computing recollection and familiarity signals, but may be engaged as a consequence of memory retrieval, like the monitoring and evaluation of retrieved information, or the top-down control for computing familiarity and recollection signals.

Electrophysiological correlates of recognition memory

In the following, we will present a selective overview of studies suggesting that familiarity and recollection can be mapped onto distinct aspects of event-related brain potentials (ERPs) recorded during the retrieval phase of recognition memory tasks. The basic logic of the ERP approach is that if familiarity and recollection are distinct cognitive processes, they should also have qualitatively distinct ERP correlates. Qualitatively distinct ERP signatures imply that dissociable neural populations have been activated by the respective experimental manipulations. Our goal is to demonstrate that electrophysiological measures are helpful in advancing psychological theories on recognition memory beyond implications derived from behavioral, neuroimaging, animal, or neuropsychological studies and, by this, can contribute to the validation of contemporary models of episodic memory. In this section, we will mainly refer to ERP findings obtained from *item* recognition memory, whereas the next section will be devoted to *associative* recognition memory. The former tasks involve distinguishing between old and new single items; the latter require retrieving particular pairings of items; e.g., pairs of test stimuli presented identically during encoding have to be distinguished from pairs of studied items that were recombined from study to test.

ERPs are computed by averaging portions of the electroencephalogram (EEG) that are related to cognitive processes elicited by particular events, such as items that are to be judged as ‘old’ or ‘new’. Thus, ERPs reflect changes in scalp-recorded electrophysiological brain activity and the amplitudes, latencies, and topographical distributions of ERP components or effects can be tied to ongoing cognitive processes. The most important virtue of this technique (beyond those of other techniques such as fMRI or PET) is its excellent temporal resolution (in the domain of milliseconds) with which functionally relevant brain processes can be monitored. Hence, the temporal onset of retrieval-related processes (such as familiarity or recollection) as revealed by ERPs can be compared to other signs of retrieval-related brain activity, as for example single-unit recordings in the monkey’s brain (Xiang & Brown, 2004). Another virtue of analyzing ERP correlates of familiarity and recollection is that these measures reflect functionally relevant brain activity in predefined experimental conditions and by this rely to a fewer extent on explicit model assumptions or model equations as the behavioral measures mentioned above.

A related approach in the electrophysiological research of human memory focuses on oscillatory behavior of neuronal systems. While EEG frequency analyses have stimulated discussions about the neurogenesis of ERP components (Makeig et al., 2002), at present measures of oscillatory brain activity as compared to ERPs still lack functional sensitivity to discriminate between experimental manipulations, and only few studies have so far used EEG spectral parameters to explicitly address theories on recognition memory (Klimesch et al., 2005; Mecklinger, Johansson, Parra, & Hanslmayr, 2007). However, recent developments in signal processing techniques have improved the signal-to-noise ratio of oscillatory brain activity as well as its functional precision, so that these measures together with ERP measures will definitely enhance our understanding of the neural processes underlying memory processes in the near future.

In anticipating the main finding of ERP studies, we would like to point out that familiarity and recollection seem to be associated with dissociable electrophysiological correlates. Specifically, familiarity is reflected in more positive going ERP deflections for studied compared to nonstudied items, with a maximum difference over frontal electrodes, approximately between 300 and 500 ms poststimulus. This effect has been termed the *mid-frontal old/new effect*. By contrast, recollection is associated with a somewhat later occurring ERP effect, namely more positive going waveforms for studied compared to nonstudied items between ca. 400 and 800 ms poststimulus. This ERP difference is termed the *parietal old/new effect* and has its maximum over (left) parietal electrodes (for reviews see Allan, Wilding, & Rugg, 1998; Curran, Tepe, & Piatt, 2006b; Friedman & Johnson, 2000; Mecklinger, 2000;

Rugg & Curran, 2007; Wilding & Herron, 2006).

Which empirical findings support the proposal that these two spatio-temporally dissociable ERP effects are specifically related to familiarity and recollection, respectively? For instance, Smith (1993) showed that the amplitude of the mid-frontal old/new effect was the same regardless of whether items have been consciously recollected or only engendered a feeling of familiarity, whereas the parietal old/new effect was enhanced when participants reported conscious recollection (see Düzel et al., 1997, for similar results). In line with behavioral studies and with the assumption that recollection is a more elaborate, effortful process than familiarity, Rugg et al. (1998) demonstrated that the mid-frontal old/new effect is insensitive to depth of processing effects (e.g., deep vs. shallow encoding), whereas the parietal effect is substantially stronger for deeply relative to shallowly encoded items.

Curran (2000) revealed that the mid-frontal old/new effect was similar for studied words and plurality-reversed lure words that were judged as ‘old’, whereas the parietal old/new effect discriminated between studied and plurality-reversed words (see also Curran & Cleary, 2003). Nessler, Mecklinger, and Penney (2001) found that the mid-frontal old/new effect was similar for true recognition of words and false recognition of semantically related but unstudied words, whereas the parietal old/new effect was greater for true than for false recognition. The findings of these studies are consistent with the proposal that false recognition of (semantically or perceptually) related lures occurs in cases of high familiarity and that, depending on task characteristics, familiarity is derived either from perceptual or conceptual similarity between study and test items. The observation that the mid-frontal effect declined when the retention interval is increased from study to test, whereas the parietal effect is not affected by this manipulation (Nessler & Mecklinger, 2003), is consistent with models of recognition memory assuming that familiarity declines more rapidly than recollection

(Yonelinas, 2002).

Düzel, Vargha-Khadem, Heinze, and Mishkin (2001) studied the amnesic patient Jon, who suffers from early and isolated hippocampal injury with apparently intact surrounding medial and lateral temporal cortices. In line with the view that recollection but not familiarity presupposes the integrity of the hippocampus, Jon shows a relatively preserved mid-frontal old/new effect, but a substantially diminished parietal old/new effect. Even though the above mentioned study did not apply adequate operational definitions of familiarity and recollection, the results support the view of dissociable neural correlates of recognition memory sub-processes. Similar results are reported by Tendolkar et al. (1999) for ten patients with reduced hippocampal volume due to Alzheimer's disease. In a source memory recognition task, the patients only exhibited the mid-frontal but not the parietal old/new effect that was present in healthy controls.

Curran (2004) demonstrated that dividing attention during encoding reduces the parietal, but not the mid-frontal old/new effect. This finding supports the assumption that familiarity operates more automatically than recollection. Consistent with results that the amnestic drug midazolam impairs behavioral estimates of recollection more so than those of familiarity, Curran, DeBuse, Woroch, and Hirshman (2006a) showed that the drug selectively diminished the parietal old/new effect compared to a saline control condition, whereas the mid-frontal old/new effect was unaffected.

Using two different categories of ’old’ responses by which participants could indicate either partial or full retrieval of the study episode, Vilberg, Moosavi, and Rugg (2006) showed that the parietal old/new effect is greater when participants can recollect larger amounts of information, whereas the mid-frontal old/new effect is insensitive to the amount of information recollected. Woodruff, Hayama, and Rugg (2006) found that single words engendering feelings of familiarity in the absence of recollection elicited a mid-frontal but no parietal ERP old/new effect. The former effect also varied with the strength of the familiarity signal, operationally defined as the confidence with which an ’old‘ response was given. By contrast, words that were reported to be accompanied by recollection of specific contextual details elicited an additional parietal old/new effect that was not modulated by familiarity. The findings of these two studies indicate that the mid-frontal old/new effect varies as a function of familiarity strength, whereas the parietal old/new effect is specific for recollection. The assumption that familiarity reflects a strength-like signal and that ’old‘ decisions are made when familiarity exceeds a response criterion also implies that familiarity should contribute to ’old‘ decisions to a larger extent when a conservative rather than a liberal response criterion is selected. In support of this assumption, Azimian-Faridani and Wilding (2006) showed that under a conservative response criterion, the waveforms in the 300 to 500 ms time interval to hits and correct rejections at frontal recordings were more positive going than under a liberal response criterion.

In a recent series of experiments conducted in our lab, we further tested the functional characteristics of the ERP correlates of familiarity and recollection using morphed faces as stimulus materials. An interesting feature of the morphing procedure is that each face can be continuously transformed in any other face (see Jäger, Seiler, & Mecklinger, 2005). This allows examining the impact of even subtle changes in face similarity between study and test. In one study (Kipp, Jäger, & Mecklinger, 2006), sixteen participants performed an item recognition task for face stimuli. The key experimental manipulation was that the test phase included old faces and faces that, though physically different from study faces, preserved person identity from study to test (see Figure 1 for illustration): As revealed by a pilot rating study, 35% morphed faces were still perceived as representing the *same* person as the parent (i.e., 0% morphed) face, although the faces could reliably be discriminated on a physical level (Jäger et al., 2005). By contrast, 70% morphed face stimuli were typically judged to depict *different* persons as the parent faces. Participants were required to respond ‘old’ whenever they recognized a *person* that was memorized during the study phase (i.e., 0% and 35% morphed faces) and to respond ‘new’ when they encounter a person previously unseen (i.e., 70% morphed and new faces)[1].

Insert Figure 1 about here

We hypothesized that repeated faces (i.e., 0% morphed faces), should elicit typical mid-frontal and parietal old/new effects, as recognition of such faces can be based on familiarity and/or recollection. By contrast, for 35% morphed faces correctly classified as ‘old’, we expected high levels of familiarity, as slightly morphed faces share strong similarities (and highly overlapping anterior MTLC representations) with faces that were actually studied. As these faces did not appear in the study phase, no recollection of the study context and by this no parietal old/new effect was expected. For 70% morphed faces judged as ‘new’, we expected no reliable mid-frontal or parietal old/new effects, as these face stimuli did not share physical or identity features with the studied 0% morphed faces.

Behavioral results revealed high hit rates for repeated faces (90% ‘old’ responses) and 35% morphed faces (79% ‘old’ responses). In addition, the majority of the 70% morphed faces were rejected as ‘new’ persons (75% ‘new’ responses) and participants were accurate in rejecting completely novel face stimuli (84% ‘new’ responses).

As can be seen in the middle row of Figure 2, we obtained a broad old/new effect with a maximum at mid-frontal (i.e., Fz) electrodes between 400 and 600 ms poststimulus. The topographical map for this mid-frontal old/new effect reflects the contrast between repeated faces and the average of 70% morphed and novel faces. Moreover, results shown in the lower row of Figure 2 revealed a left parietal old/new effect (i.e., P5) between 600 and 800 ms for old faces but not for 35% morphed faces. The topographical map for this parietal old/new effect reflects the contrast between repeated and 35% morphed faces.

Insert Figure 2 about here

In line with our expectations, these data indicate that both familiarity and recollection contributed to item recognition judgments for repeated face stimuli, as revealed by the presence of mid-frontal and left parietal old/new effects. As both effects were differentially modulated by morphing degree, the following conclusions are warranted: Repeated faces and 35% morphed faces that preserved face identity could be judged as ‘old’ because they were accompanied by feelings of familiarity, as reflected by the presence of a mid-frontal old/new effect. Note that we initially expected the 35% morphed faces to elicit equal familiarity levels as repeated faces, because we did not expect familiarity signals to be diagnostic or sensitive for such subtle perceptual modifications. However, the results revealed a graded mid-frontal old/new effect for 35% morphed compared to repeated faces[2]. Together with the higher hit rate for repeated than for 35% morphed faces, the finding of a graded frontal old/new effect is consistent with the view that familiarity relies on a continuously distributed strength-like memory process, whereby ‘old’ responses are given when memory strength exceeds a certain criterion. Interpreting this finding in terms of the strength models of familiarity with overlapping distributions of ‘old’ and ‘new’ items (Yonelinas, 1997), it appears that the familiarity distribution of 35% morphed faces, as compared to the distribution of repeated faces, is somewhat shifted towards the distribution of novel faces. However, a substantial proportion of both distributions (i.e., those of 35% morphed and repeated faces) seem to exceed the response criterion to the right and thus lead to correct ‘old’ judgments (Quamme, 2004; Yonelinas, 1997, 2001). Graded mid-frontal old/new effects have also been reported in experiments that systematically varied study-test similarity by presenting mirror-reversed versions of studied objects at test (Groh-Bordin, Zimmer, & Mecklinger, 2005) or by varying the study modality (spoken words/objects) of visually tested objects (Mecklinger, 2006). Taken together, these studies provide strong support for the view that the information supporting familiarity-based recognition is a continuously varying strength-like signal.

By contrast, a parietal old/new effect was exclusively elicited by identically repeated faces. The absence of a parietal old/new effect for 35% morphed faces is consistent with the view that recollection relies on a threshold process, by which only repeated items exceed a response threshold, whereas for 35% morphed faces though generating strong feelings of familiarity, no episodic information was actually recollected. It also seems that the 35% morphed faces represent insufficient retrieval cues for the elicitation of (immediate) recollections about the *parent* faces that were initially memorized.

Interestingly, as shown in the upper row of Figure 2, our study revealed an additional early (300 to 400 ms) ERP effect at fronto-polar recordings sites (i.e., Fpz). This effect discriminated faces classified as ‘old’ (i.e., repeated and 35% morphed faces) from faces receiving a ‘new’ response (i.e., 70% morphed and novel faces)[3]. The topographical map for this anterior-frontal old/new effect between 300 and 400 ms reflects the contrast between the average of repeated and 35% morphed faces and the average of 70% morphed and novel faces. ERP old/new effects with similar anterior-frontal distributions and even earlier onset latencies (at around 200 ms) have been reported in a variety of recent studies (Curran & Dien, 2003; Ecker, Zimmer, Groh-Bordin, & Mecklinger, in press; Jäger, Mecklinger, & Kipp, 2006; Tsivilis, Otten, & Rugg, 2001). Early repetition effects are often found when short or even zero lag repetition intervals are used (Penney, Mecklinger, & Nessler, 2001; Rugg & Nieto-Vegas, 1999). With longer intervals as in the present study, these effects seem to be modality-specific. Even though a functional account of these early fronto-polar ERP effects is still missing and it is unclear to what extent they reflect implicit priming mechanisms or are more exclusively related to explicit memory tasks (see Curran & Dien, 2003, for a discussion), it is conceivable that they are associated with differential novelty processing and/or priming processes that contribute to intentional and explicit memory retrieval. Further studies will be required to elucidate in more detail how these early effects are functionally related to the mid-frontal and parietal old/new effects, i.e., the putative correlates of familiarity and recollection.

Taken together, our study revealed that the mid-frontal and the parietal old/new effect respond differentially to subtle perceptual manipulations, indicating that slightly altered faces elicit feelings of familiarity in the absence of recollection of episodic information. A real-life example of such experiences may be a situation in which we encounter a person after several years. Due to advanced biological age and other changes, the appearance of the person may have altered to some degree. In this situation, we may very likely have feelings of ‘knowing’ the person from somewhere, but may not immediately recall specific information such as the person’s name or the circumstances in which we were dealing with the person.

In concluding this section on ERP correlates of item recognition memory, our selective review of ERP investigations carried out in different laboratories with different stimulus materials and experimental setups indicates that the mid-frontal and the parietal old/new effect can indeed be associated with familiarity and recollection, respectively. From the converse point of view, it also seems clear that ERP studies can be helpful for constraining and verifying psychological theories. For instance, the dissociation of the two old/new effects and their corresponding characteristics strongly suggests the existence of two functionally distinct mechanisms underlying recognition memory, as proposed by formal dual-process models. A neural dissociation of familiarity and recollection is also strong evidence against single-process models of recognition memory and enables inferences on the neurocomputational mechanisms of distinct neural populations contributing to our ability to recognize previously encountered information.

Electrophysiological correlates of associative recognition memory

This section will focus on associative (rather than item) recognition memory. As the starting point of the following discussion, we want to point to the fact that the dual-process account makes relatively strong claims about the underlying mechanisms of item versus associative recognition memory (Yonelinas, 2001, 2002). Specifically, both familiarity and recollection are assumed to support item recognition judgments, as stimuli can be judged ‘old’ if participants recollect information about the study episode or if an item is sufficiently familiar. By contrast, only recollection but not familiarity is assumed to support associative recognition judgments, as individual stimuli are equally familiar in both intact and recombined pairs and thus familiarity cannot be diagnostic to distinguish between them. Therefore, accepting intact or rejecting recombined pairs is thought to require recollection for the particular pairings of stimuli. The theoretical assumption that familiarity cannot support associative recognition memory arises from the view that familiarity reflects neural activation of single items (Yonelinas, 2002) that are represented in anterior MTLC (Norman & O'Reilly, 2003). From the assumption that the hippocampus but not the anterior MTLC is able to encode and retrieve associations between arbitrarily paired items, it follows that hippocampal recollection is imperatively needed for the retrieval of such associations.

The hypothesis about the differential contributions of familiarity and recollection to tests of item and associative recognition memory is consistent with a number of findings. First, whereas item recognition typically elicits both a mid-frontal and a parietal old/new effect, associative recognition memory is found to trigger a parietal old/new effect only (Donaldson & Rugg, 1998, 1999). Second, ROCs are typically curvilinear and asymmetrical along the diagonal for item recognition, but relatively linear for associative recognition memory tasks (Yonelinas, 1997). These shapes reflect contributions of continuously varying familiarity signals and threshold-like recollection to item recognition, but isolated contributions of recollection to associative recognition memory. Third, amnesic patients with impairments in recollection due to hippocampal lesions but spared familiarity often show no or only small deficits in item recognition, but substantial impairments in associative recognition memory (e.g., Holdstock et al., 2005; Mayes et al., 2004). Finally, speeded old/new judgments (thought to mainly reflect familiarity) provide accurate item recognition but unreliable associative recognition performance (Hintzman, Caulton, & Levitin, 1998).

Although these findings on the first glance fit in well with theoretical assumptions on the neurocomputational bases of familiarity and recollection, the claim that familiarity cannot support the retrieval of associations is not without counterarguments and controversially discussed (see Aggleton & Brown, 2006; Mecklinger, 2006; Yonelinas, 2002). Specifically, the current debate concerns the potential circumstances under which familiarity can support associative recognition judgments. One hypothesis formulated by Yonelinas and colleagues (Yonelinas, Kroll, Dobbins, & Soltani, 1999; see also Quamme, 2004; Quamme, Yonelinas, & Norman, 2007) and adopted and extended by other authors (Giovanello, Keane, & Verfaellie, 2006; Jäger et al., 2006; Rhodes & Donaldson, 2007) posits that familiarity can contribute to associative recognition memory given that the to-be-associated stimuli are encoded as a coherent whole and form a bound or ‘unitized’ representation. *Unitization* refers to conditions in which two or more previously separate items are strengthened with experience and become represented as a single unit (Hayes-Roth, 1977; Cesaro, 1985; Graf & Schacter, 1989). By this, unitary structures - other than associative structures - can be perceived and remembered as one entity, i.e., they result in unitary memory traces (e.g., facial features that are bound together to form a single face). This idea, hereinafter referred to as the *unitization hypothesis* (Quamme, 2004), suggests that associations can be retrieved independently from hippocampal recollection given that the associations are unitized within the anterior MTLC. This may be possible when to-be-associated items are perceived as a coherent entity, like pairs of items that frequently co-occur and thus share strong pre-experimental associations (e.g., word-pairs such as *sea-food* or *traffic-jam*; Giovanello et al., 2006; Quamme, 2004; Rhodes & Donaldson, 2007), or when unrelated items are encoded as if they referred to a single object (Quamme, 2004; Quamme et al., 2007).

The view that associative memories differ in the degree to which their components can be unitized and by this can create memory representations that support either familiarity or recollection has also recently been postulated by Mayes, Montaldi, and Migo (2007; see also Mayes et al., 2004). In addition to unitized (intra-item) associations (e.g., the entity of a face), the model assumes that also within-domain associations composed of similar but not unitized items (e.g., two faces or a table and a chair) can be supported by familiarity. Empirical evidence for this view comes from a single amnesic patient (Y.R.), who shows selective hippocampal atrophy. She demonstrates selective impairments in associative recognition for between-domain associations, but sparing of unitized and within-domain associations. The intact performance for within-domain associations has been taken to reflect that familiarity can support associative recognition even in the absence of unitization (the implications of this view will be discussed later).

One source of evidence for the assumption that unitization can create familiarity-supporting memory representations comes from studies that used strongly pre-experimentally integrated items. Opitz and Cornell (2006) required participants to memorize four words in each study trial (e.g., *oasis, camel, chair, desert)*. In two encoding conditions, participants either indicated which word did not fit in the associative context of the other three words (the associative condition) or indicated which of the four words denoted the smallest object (the relational condition). The objective behind this manipulation was that only the associative condition should promote the encoding of pre-existing semantic associations between words. During the test phase, studied words of both conditions and new words were presented as retrieval cues. Results revealed a mid-frontal old/new effect in the associative but not in the relational condition. As the mid-frontal old/new effect in the associative condition was enhanced for those words for which the complete word triplet was retrieved, the results argue against the view that enhanced memory strength for words encoded in the associative condition (i.e., item memory) may have contributed to the differences in the mid-frontal old/new effect. Rather, the results are consistent with the view that activation of pre-existing semantic relationships during encoding can create familiarity-supporting memory representations.

In another recent ERP study, Greve, van Rossum, and Donaldson (2007) found a mid-frontal old/new effect for word-pairs that had to be discriminated from recombined and new word-pairs only when the word-pairs were semantically related, again supporting the view that pre-existing semantic knowledge can be used to form unitized memory representations that support familiarity-based recognition.

However, in contrast to these findings, Rhodes and Donaldson (2007) did *not* find that familiarity supports associative recognition judgments for solely semantically related word-pairs (e.g., *prince-duke*). Rather, the results specifically supported the unitization hypothesis, as a mid-frontal old/new effect was elicited for word-pairs sharing a strong association and were rated as having the most unitized representation (e.g. *traffic-jam; glow-worm*). The effect was absent for purely semantic pairings (e.g., *cereal-bread*). However, an objection against the “unitization-supports-familiarity” interpretation in the latter two studies could be that rather than contrasting same and rearranged pairings – a common practice in associative recognition memory research – the authors compared same pairings with new pairings, such that contributions of differential memory strength of single words to the mid-frontal old/new effect cannot be excluded.

Another approach for testing the validity of the unitization hypothesis is to use arbitrarily paired items and to manipulate unitization by study manipulations that either encourage or discourage forming a single entity. Rather than relying on pre-experimental knowledge, this approach bears the advantage that it allows to directly examine whether unitization effects on familiarity-based recognition can be initiated by the type of processing engaged at encoding. By this, it enables investigating the learning mechanisms and the kind of memory representations they generate. Using unrelated word-pairs as study materials, Quamme et al. (2007) examined the impact of encoding processing on associative recognition memory. Word-pairs were either studied as separate parts of sentences or as newly learned compounds. Amnesic patients, who had previously demonstrated impaired recollection and spared familiarity, showed a memory advantage in the compound (unitization) condition over the sentence condition. When testing conditions were changed to restrict responses to familiarity, the same advantage of unitization at study was found for normal controls.

In a recent ERP study, we investigated the unitization hypothesis in more detail (Jäger et al., 2006). Using an associative recognition memory task for face-pairs, we aimed to examine the circumstances under which face parts are unitized in a way that they form familiarity-supporting memory representations. In one condition, participants memorized pairs of sequentially presented face stimuli depicting two different persons (the *inter-item* condition). During a subsequent test phase, participants initially had to judge a *single test face* as ‘old’ or ‘new’. Thereafter, for correctly identified old faces, a forced-choice judgment was required in which participants had to indicate which of two studied faces presented side by side was initially paired with the single test face during the study phase, by this probing memory for the association of the two study faces.

On the basis of the dual-process account, and consistent with previous findings on associative recognition memory (Donaldson & Rugg, 1998, 1999; Yonelinas, 1997), we expected performance in the inter-item condition to mainly rely on recollection, as the binding and retrieval of arbitrarily paired faces is proposed to strongly depend on hippocampal recollection, whereas anterior MTLC familiarity cannot be diagnostic for such associative judgments (Norman & O’Reilly, 2003; Quamme, 2004). In other words, we expected a strong parietal but no mid-frontal old/new effect in this condition. This effect should also be larger for hits followed by correct relative to incorrect associative (i.e., forced-choice) judgments.

In a second condition (the *intra-item* condition), in which participants also memorized pairs of physically different faces, the faces were rated to depict the same person to a high degree. The face stimuli were again created by a morphing software (Jäger et al., 2005). The face-pairs of this condition consisted of either 35% plus 0% or 100% plus 70% morphed faces drawn from the same morph-continua, but presented in separate study trials. By this, it was possible to present 35% morphed faces as single test faces in the test phase, and their 0% and 70% morphed versions for the forced-choice judgments. Notably, as the 0% and 70% morphed faces were equally distant in morphing degree from the 35% faces, forced-choice judgments could not be made solely on the basis of differences in face similarity, but instead required retrieving associative memory representations established during encoding.

Our hypotheses regarding the intra-item condition were as follows: As to-be-associated face stimuli contained highly overlapping features and could be bound together in a way that they are perceived as a single person, encoding of such face-pairs and their features presumably engages unitization processes in anterior MTLC. These unitized representations may involve enhanced activation of the two images' overlapping features and reduced activation of nonoverlapping ones (a process termed "sharpening"; Norman & O'Reilly, 2003) and should thus support familiarity-based recognition. We expected a reliable mid-frontal old/new effect during old/new judgments of faces that should be larger for correct than for incorrect associative (forced-choice) judgments. By contrast, recollection may not be capable of supporting associations in the intra-item condition, as recollection is suggested to break down when the overlap between to-be-associated information is too high, because pattern-separated representations cannot be established in this case (Schacter et al., 1998). In consequence, an attenuated or at least significantly smaller parietal old/new effect was expected compared to the inter-item condition in which recollection is assumed to play the most critical role.

Insert Figure 3 about here

Performance (old/new discrimination and associative judgments) was better in the intra- than in the inter-item condition. As can be seen in Figure 3, in the *intra-item* condition there was a mid-frontal old/new effect between 300 and 400 ms poststimulus (see electrode Fz). Consistent with our hypothesis that unitization of face features across both faces forms familiarity-supporting associative memory representations, this mid-frontal old/new effect was significantly greater for hits followed by correct relative to incorrect associative judgments. By contrast, no parietal old/new effect (measured between 400 and 700 ms) was apparent in this condition (see electrode Pz). Conversely, in the *inter-item* condition, there was no reliable mid-frontal old/new effect. However, a pronounced parietal old/new effect emerged between 400 and 700 ms, which, confirming our predictions, was significantly larger for hits followed by correct relative to incorrect associative judgments.

To summarize, we obtained a double dissociation of the ERP correlates of familiarity and recollection. The mid-frontal old/new effect was significantly larger in the intra- compared to the inter-item condition, whereas the parietal old/new effect was significantly larger in the inter- compared to the intra-item condition. Notably, confirming the view that both effects reflect associative recognition memory, the mid-frontal and the parietal old/new effect discriminated correct from incorrect associative judgments. Consistent with our hypotheses, familiarity supported associative recognition judgments given that the to-be-associated stimuli were unitizable, i.e., in the intra-item condition, whereas recollection seemed to break down in this condition, presumably because the overlap between to-be-associated stimuli was too high. Conversely, in the inter-item condition associative recognition memory was supported by recollection, whereas similarly to previous studies familiarity did not seem to contribute to recognition judgments at all, presumably because familiarity is not diagnostic for distinguishing between correct and incorrect arbitrary face-pairings. Moreover, the finding of two spatio-temporally and functionally dissociable ERP old/new effects strongly supports dual- (rather than single-) process models of recognition memory.

Notably, the absence of a mid-frontal old/new effect in the inter-item condition, in which the association of two very similar items (i.e., two faces) had to be memorized, sheds some light on the limits of unitization mechanisms and the formation of familiarity-supporting memory representations. Unitization processes seem to rely on an entity-creating framework (the layout of a face or a semantic concept) into which items can be integrated. This view is also supported by a recent animal study on memory consolidation, showing that the presence of an associative schema (i.e., a fixed spatial arrangement) into which new information (i.e., flavors) can be encoded, allows the consolidation of new memory traces even after one trial learning in hippocampal-lesioned animals (Tse et al., 2007).

It has also been argued that objective criteria for unitization have to be established (see Ceraso, 1985, for a proposal) and that inferring unitization from the presence of familiarity-based recognition bears the risk of circularity (Mayes et al., 2007). The pre-experimental ratings of facial and personal identity for the morphed faces in the present study or the unitization ratings employed for word-pairs (Rhodes & Donaldson, 2007) in our view would meet such criteria for objective measures of unitization. The view expressed by the unitization account, namely that items to be recognized may combine with other items to higher order units with emergent properties was not only at the heart of the work of early Gestalt psychology (Ceraso, 1985). It is also of central relevance in other and broader models of knowledge representation (Hayes-Roth, 1977). From a memory retrieval point of view, an important and interesting feature of unitized representations is that they allow “redintegration”, a process by which a whole memory representation can be reinstated by a partial cue (Horowitz & Prytulak, 1969). Such a process is less likely for associative structures, where a partial cue usually leads to the retrieval of parts of a memory trace.

To summarize, extending the classically held view that associative memory relies on recollection without benefiting from familiarity, recent studies suggest that associative memories differ in the degree to which their components can be bound by anterior MTLC or hippocampal structures, respectively. Items that can be unitized and represented as a single entity can form memory representations that support familiarity-based recognition, whereas arbitrary or even similar components that cannot be bound together to form an entity form recollection-supporting memories. Anterior MTLC structures centered on the perirhinal cortex and the hippocampus by means of their neurocomputational mechanism can be considered as the most likely neural substrates for the two forms of associative memories.

Pre-experimentally unitized associations (e.g., *traffic-jam*) and associations that were unitized by encoding instructions can form familiarity-supporting memory representations. This view not only implies that processes engaged during encoding play an important role for unitization, it also raises the question whether pre-experimental and long term unitization processes that lead to semantic knowledge structures and unitization induced by an encoding trial rely on the same or on distinct neurocomputational mechanisms. In terms of the Norman and O’Reilly (2003) model, one may speculate that semantic knowledge may have arisen from long-term sharpening. In other words, the repeated exposure to specific item combinations may have enhanced the binding of these items and reduced the binding to others, resulting in lower neural responsiveness in anterior MTLC. A critical role of anterior MTLC structures for semantic processing is also demonstrated by intracranial recordings (Fernandez, Klaver, Fell, Grunwald, & Elger, 2002; Meyer et al., 2005). By this, items that were unitized (by means of a sharpening mechanism) into a single entity by encoding processes (single trial learning) as well as semantically related items (long-term learning) are interconnected in anterior MTLC, which enables associative retrieval independent from the hippocampus in both cases.

Within the discussion of the contributions of familiarity and recollection to associative recognition memory, it is worth referring to a somewhat related line of research examining the sensitivity of familiarity for *contextual influences*. While some situations may require familiarity-based recognition of unitized associations, such as encountering a person after a long time, other real world situations, like seeing an object in many different contexts, require familiarity to be item-specific and acontextual. Some findings of ERP studies indeed indicate that familiarity is sensitive for influences of contextual information, by this challenging the common assumption that familiarity represents an acontextual, item-specific form of recognition memory that should not be influenced by contextual information. Specifically, Tsivilis et al. (2001) reported that during item recognition the mid-frontal old/new effect was attenuated when to-be-judged objects were superimposed on novel, but irrelevant backgrounds. Using the same paradigm, Piatt, Curran, Collins, and Woroch (reported in Curran et al., 2006b) found that the mid-frontal old/new effect was more pronounced when object-background pairings were the same as in the study phase than when they were rearranged into novel pairings of studied objects and studied backgrounds.

However, in a recent study by Ecker et al. (2007), these contextual influences on the mid-frontal old/new effect disappeared when participants were specifically instructed to prevent directing attention to the (task-irrelevant) backgrounds and to focus attention exclusively on the objects when judging their old/new status. In light of these findings, it is reasonable to assume that previously found context effects on item familiarity are mediated by attentional and/or perceptual factors (e.g., attention directed towards backgrounds or impoverished figure-ground segmentation). This is consistent with the theoretical view that familiarity subserves genuinely acontextual forms of recognition memory. Depending on the situational characteristics, features of an episode may either be bound and retrieved as a coherent entity or attentional processes may render some features more salient and prevent contextual influences on familiarity-based recognition.

Conclusions: Open issues and directions for future research

Although many studies have started to unravel the neurocognitive processes underlying our ability to recognize previously encountered information and have added to the converging evidence on the putative ERP correlates of familiarity and recollection, there are many open and timely questions that may be addressed in future (ERP) studies.

A first avenue for further ERP research may be to critically examine theoretical assumptions on the functional characteristics of familiarity and recollection. Findings from ERP studies generally agree with the assumption that familiarity is available earlier than recollection (Mecklinger, 2000) or that familiarity operates more automatically than recollection (Curran, 2004). However, other model assumptions have not been extensively tested, such as the view that familiarity and recollection represent *independent* memory processes. Note that this assumption may be hard (if not impossible) to test in behavioral studies, because the most important techniques for estimating familiarity and recollection a priori rely on the independence assumption. Also, the independence assumption would predict that certain brain lesions should lead to a loss of recollection and a sparing of familiarity, whereas other lesions should produce the opposite pattern. However, such a double dissociation is hard to find in clinical populations. Even though lesions restricted to the hippocampus in most cases remove the recollection component while sparing familiarity, the opposite pattern is very rarely found. Lesions restricted to the anterior MTLC region while sparing the hippocampus are not only hard to find. As the parahippocampal region is the main input zone for the hippocampus, lesions to this area should also disconnect the hippocampus from surrounding areas and by this attenuate recollection (Aggleton & Brown, 2006).

By contrast, ERP measures are not constrained by model assumptions, do not rely on the size and location of brain lesions, and can easily be recorded from non-clinical populations. By this, ERPs may be well suited for testing the independence assumption. Indeed, findings of ERP studies seem to confirm that familiarity and recollection can occur independently, as in some conditions a mid-frontal but no parietal old/new effect is observed (Curran et al., 2006a; Düzel et al., 2001; Jäger et al., 2006; Woodruff et al., 2006), whereas in other conditions the parietal old/new effect is exclusively elicited (Donaldson & Rugg, 1998, 1999; Jäger et al., 2006; Opitz & Cornell, 2006; Rhodes & Donaldson, 2007; Yovel & Paller, 2004). Moreover, double dissociations between the mid-frontal and the parietal old/new effects have recently been demonstrated within the same experimental setup (Jäger et al., 2006; Woodruff et al., 2006). These findings indicate that familiarity and recollection operate independently, with their relative contributions presumably relying on specific demands of the task at hand. A situation in which a retrieval cue elicits recollection without familiarity may be intuitively hard to imagine. Why should an episode that we retrieve in great detail not also be familiar? From the independence assumption, however, it follows that recollection can either co-occur or take place independently from familiarity. Recollection without familiarity may for example be a direct consequence of the computational mechanisms underlying both forms of remembering. How exactly features or items processed in anterior MTLC converge to form a familiarity-supporting memory representation is still unclear. However, the independence assumption together with empirical findings suggests that hippocampus-based recollection should become more and more relevant the less unitization of information occurs in anterior MTLC. This view also implies that specific task instructions, e.g., the specificity with which information has to be retrieved upon presentation of a retrieval cue, such as discriminating old from equally familiar recombined pairs of items, may also promote recollection-based memories without engaging familiarity. Future studies will be required that more specifically address the issue under which conditions familiarity and recollection operate independently.

Another interesting issue is whether familiarity and recollection can be elicited automatically, even if a task does not explicitly entail the retrieval of previous episodes (e.g., in implicit memory tasks). From a real-world view, one may expect that feelings of familiarity or recollective experiences do not depend on the prerequisite that one’s cognitive system is explicitly prepared for treating stimuli as episodic retrieval cues, a state termed *retrieval mode* (Wilding & Herron, 2006). From the theoretical view, familiarity is considered to occur relatively automatically, but recollection is supposed to involve more effortful operations. From this it follows that familiarity signals should not depend on top down processes that set up retrieval modes. However, a recent study by Groh-Bordin et al. (2005) examining ERP correlates of explicit and implicit memory suggests that familiarity signals may indeed depend on the adaptation of a retrieval mode. Findings revealed a mid-frontal and a parietal old/new effect in the explicit memory task in which participants had to make old/new judgments about visually presented objects. By contrast, neither of these ERP effects was apparent in an implicit memory task in which participants had to make living/nonliving judgments about novel and repeated objects. Rather, a late occipitoparietal repetition effect was found that could be topographically dissociated from the parietal old/new effect in the explicit task. These finding suggests that neither familiarity nor recollection signals are elicited in implicit memory tasks in which the brain is not set up for treating external events as episodic retrieval cues, but are rather contingent upon the adoption of a retrieval mode in order to be initiated. Hence, familiarity does not seem to be automatic in such a sense that it can occur even in tasks in which no reference to previous occurrences of stimuli is made.

A hint towards the role of top-down processes during memory retrieval comes from single-unit recordings in monkeys. Neuronal responses signaling stimulus familiarity in a serial recognition task were found in the medial and ventral prefrontal cortex (Xiang & Brown, 2004). Interestingly, these responses had about the same onset latencies (200 to 300 ms) as the scalp recorded mid-frontal old/new effect and were considerably longer than the earliest neuronal responses to familiarity in the inferior temporal lobes (Li et al., 1993). This implies that prefrontal activation cannot be the source of anterior MTLC responses to familiarity, whereas later portions of anterior MTLC responses might well be modulated by PFC responses. Taken together, these data suggest that familiarity is triggered early and automatically by appropriate sensory input to anterior MTLC, but only if the brain is prepared to treat this input as cues for episodic retrieval, familiarity-based recognition occurs. Otherwise, as in implicit memory tests, these early discharges may initiate other processes and facilitate performance, but do not lead to the formation of familiarity-supporting memory representations. Another important implication of the above mentioned single-unit studies is that medial and ventral prefrontal regions together with anterior MTLC regions may be involved in the generation of the scalp-recorded mid-frontal old/new effect. Further studies are warranted that examine the role of top-down processes in initiating and guiding memory retrieval processes and the computation of familiarity and recollection signals as well as the neural networks generating the scalp recorded old/new effects.

Although there is substantial evidence linking a mid-frontal and a parietal old/new effect to familiarity and recollection, respectively, there are also findings challenging this proposal (see Curran et al., 2006b, for a discussion). For instance, Finnigan, Humphreys, Dennis, and Geffen (2002) found an early 300-500 ms old/new effect (over left parietal electrodes) that was linked to memory strength, by this resembling the concept of familiarity. However, a later 500-800 ms parietal old/new effect typically associated with recollection was taken to reflect the accuracy or confidence of memory decisions rather than recollection. Another account of the mid-frontal old/new effect is provided by Paller and colleagues. In one of their studies (Yovel and Paller, 2004) participants had to learn associations between unfamiliar faces and occupations. Familiarity-based recognition was inferred when participants recognized faces without retrieving any further information such as their associated occupations. By contrast, recollection-based recognition was assumed when participants could also recall occupations or other contextual information. Yovel and Paller (2004) found that recollection- and familiarity-based recognition were both associated with positive-going ERPs at parietal sites, revealing only a quantitative but no qualitative (e.g., topographical or temporal) difference between the two types of recognition responses. Hence, these findings suggest that recollective and familiarity-based recognition are mediated by the same neural network. On the basis of this study and other findings, Paller and colleagues propose that the mid-frontal old/new effect reflects conceptual priming rather than familiarity. (see Paller, Voss, & Boehm, 2007, for a review).

However, several lines of evidence argue against the view that the mid-frontal old/new effect reflects conceptual priming. First, a replication of the Yovel and Paller (2004) study with a different set of face stimuli revealed a reliable mid-frontal old/new effect for (familiar) faces retrieved without their associated occupations (Curran & Hancock, 2007). Second, arguing against the conceptual priming account of the mid-frontal old/new effect, a variety of studies using non-conceptual stimuli, like meaningless geometrical shapes (Curran, Tanaka, & Weiskopf, 2002; Groh-Bordin, Zimmer, & Ecker, 2006) or unfamiliar faces (Nessler, Mecklinger, & Penney 2005; Johansson, Mecklinger, & Treese, 2004) found the effect. Finally, the mid-frontal old/new effect is modulated by variables affecting recognition memory, like the adaptation of a response criterion (Azimian-Faridani & Wilding, 2006), signal strength (Woodruff et al., 2006), or study-test similarity (Curran, 2000; Nessler et al., 2001). These modulations are difficult to account for by the view that the mid-frontal old/new effect is a reflection of conceptual priming.

Another issue to be further addressed is the question about the circumstances under which familiarity contributes to associative recognition memory (Aggleton & Brown, 2006; Mayes et al., 2007). As outlined in this chapter, there is growing evidence for the unitization hypothesis, i.e., the assumption that familiarity can support associative recognition judgments given that items or features are unitized into single entities. Also, using encoding conditions that encourage holistic processing, unitization seems to be possible for arbitrary items. However, findings of whether familiarity also supports associative retrieval of pre-experimentally unitized (semantic) associations have been somewhat mixed and deserve further investigation. With regard to the unitization view, future studies may specifically tackle the boundary conditions under which unitization can take place. Do items that are unitizable have some particular characteristics, such as being perceptually highly overlapping or being encodable in entity-creating frameworks? What are the encoding conditions that allow unitization of completely arbitrary items? Can unitization also occur for pairs of items of different modalities or is unitization constrained to visual stimuli represented in close proximity within anterior MTLC? As the anterior MTLC receives input from polymodal association cortices (Suzuki, 1996), the formation of unitized memory representations should not be limited to the visual modality.

In conclusion, although behavioral, animal, neuropsychological, neuroimaging, and electrophysiological studies have disclosed exciting findings on the puzzle about the cognitive processes underlying our ability to recognize previously encountered information, many issues remain to be resolved and provide the basis for questions addressed in future studies on recognition memory.

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Footnotes

Footnote 1. After old/new decisions participants were also required to make physical judgments about whether or not the face stimuli judged as ‘old’ were physically identical to the memorized face stimuli. However, there were too few trials to allow separate ERP analyses for trials with correct or incorrect physical judgments, respectively.

Footnote 2.The mid-frontal old/new effect (captured at electrode Fz) was reliable for repeated and for 35% morphed faces [*t*s(15) > 4.13, *p*s < .001], but not for 70% morphed faces [*t*(15) = .93, *p* = .365], and mean amplitudes were significantly greater for repeated compared to 35% morphed faces [*t*(15) = 2.67, *p* < .05]. By contrast, the left parietal old/new effect (captured at electrode P5) was only elicited by repeated faces [*t*(15) = 2.91, *p* < .05], but not by 35% or 70% morphed faces [*t*s(15) < .50].

Footnote 3. The anterior-frontal old/new effect (captured at electrode Fpz) between 300 and 400 ms was reliable for repeated and 35% morphed faces [*t*s(15) > 2.16, *p*s < .05], with no difference between the two [*t*(15) = .51].

Figure Captions

Figure 1: Illustration of the study and the test phase of Kipp et al. (2006).

Figure 2: ERPs (shown at electrodes Fpz, Fz, and P5) and corresponding topographical maps of Kipp et al. (2006). The three time windows used to capture the anterior-frontal (300-400 ms), the mid-frontal (400-600 ms), and the left parietal (600-800 ms) old/new effects are shaded.

Figure 3: ERPs (shown at electrodes Fz and Pz) and corresponding topographical maps of Jäger et al. (2006). The two time windows used to capture the mid-frontal (300-400 ms) and the parietal (400-700 ms) old/new effects are shaded. Topographical maps reflect the difference between hits plus correct forced-choice judgments and correct rejections. ERPs and the topographical map on the left-hand side show the mid-frontal old/new effect obtained in the intra-item condition; ERPs and the topographical map on the right-hand side show the parietal old/new effect obtained in the inter-item condition. This is a modified version of a figure presented by Jäger et al. (2006).

Figure 1

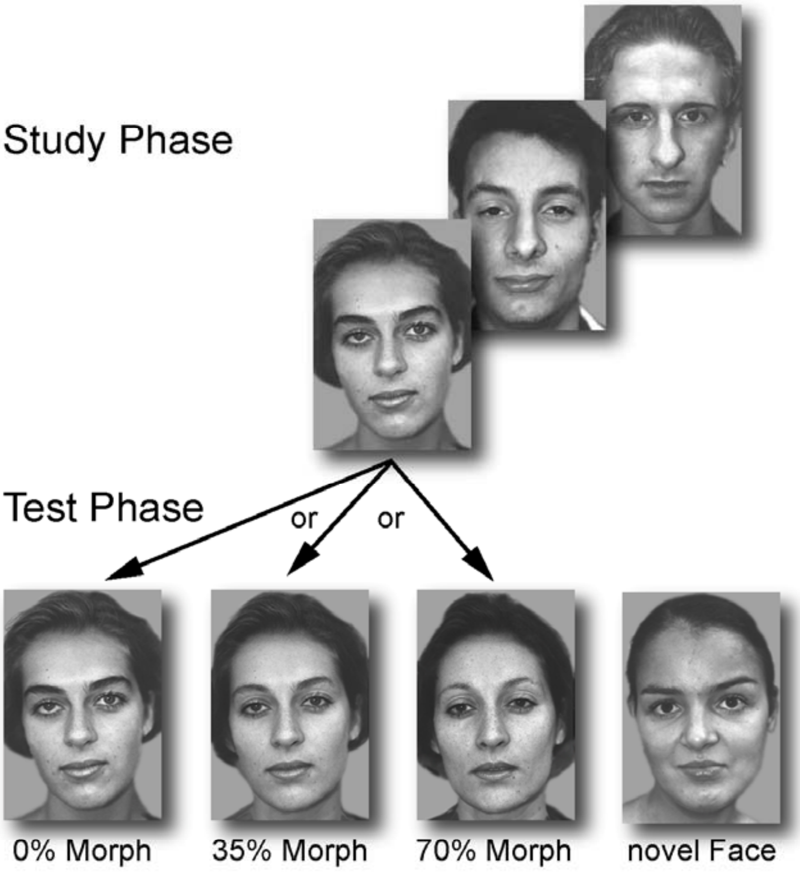

Study Phase
Test Phase
or
or
0% Morph
35% Morph
70% Morph
novel Face

Figure 2

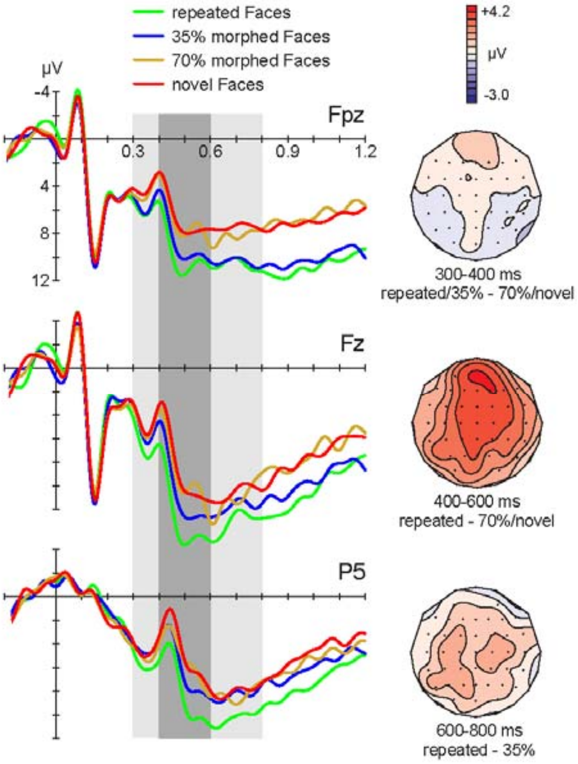
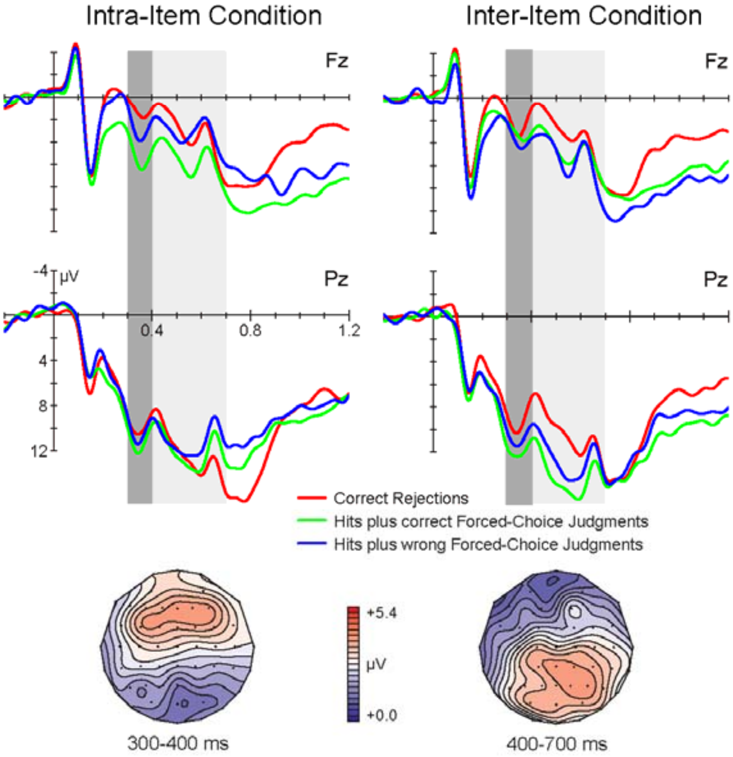

repeated Faces
35% morphed Faces
70% morphed Faces
novel Faces
µV
-4
4
8
12
0.3
0.6
0.9
1.2
Fpz
Fz
P5
+4.2
µV
-3.0
300-400 ms
repeated/35% - 70%/novel
400-600 ms
repeated - 70%/novel
600-800 ms
repeated - 35%

Figure 3


Intra-Item Condition
Inter-Item Condition
Fz
Fz
Pz
Pz
-4
μV
4
8
12
0.4
0.8
1.2
Correct Rejections
Hits plus correct Forced-Choice Judgments
Hits plus wrong Forced-Choice Judgments
+5.4
μV
+0.0
300-400 ms
400-700 ms