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Memory systems for structural and semantic knowledge of faces and buildings

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ABSTRACT

It is an ongoing debate whether specific neurocognitive systems are involved in face and object recognition, particularly for analyses that require the access to stored structural and semantic knowledge. Here we compared the processing of familiar (at the exemplar level) and unfamiliar faces and buildings by recording event-related potentials in a repetition priming paradigm. We focused on the early repetition effect (ERE/N250r) which has been proposed to indicate the access to stored structural knowledge and the late repetition effect (LRE/N400), a possible indicator of semantic knowledge. An ERE/N250r was present for familiar buildings and smaller than for faces, but indistinguishable in terms of scalp topography. In contrast, the LRE/N400 was stimulus specific in topography. These findings suggest initial access to a common store of structural knowledge followed by the activation of category-specific cortical representations of person- and building-related semantic knowledge.

1. Memory systems for structural and semantic knowledge of faces and buildings

Whether specific neurocognitive systems are involved in face and object recognition is an ongoing debate (e.g., Haxby et al., 2001; Kanwisher, 2000; Tarr and Gauthier, 2000). This issue is highly interesting because of the importance of human faces in social interaction and communication and the apparent ease of remembering and discriminating many different faces despite of their uniform basic structure. The extraordinary skills of humans in dealing with faces on their own may indicate the existence of specialized processing modules unrelated to those involved in visual object processing (e.g., McNeil and Warrington, 1993). Alternatively, face and object recognition may be mediated by the same neurocognitive systems with differences between faces and non-face objects arising from specific demands on these systems (e.g., Tarr and Cheng, 2003).

Functional models of face and object recognition follow similar lines. In the widely accepted model of face recognition by Bruce and Young (1986) the initial processing stages include pictorial and structural encoding, providing the necessary information, among others, for the so-called face recognition units (FRUs). In FRUs the products of structural encoding are matched with stored structural representations of known faces. Information from the activated FRUs facilitates the access to person identity nodes (PINs), from where identity-specific semantic information and the names of persons can be activated. Object recognition models (e.g., Ellis and Young, 1996) posit that after perceptual and structural encoding of an object, its structural representation is matched to representations stored in object recognition units (ORUs). This allows the

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access to semantic representations and name retrieval. The present study focuses on processes related to accessing stored structural representations and identity-specific semantic information. In the following we will describe proposed similarities and differences in face and object recognition in terms of cognitive and neuronal processes taking place at these stages.

1.1. *Pictorial and structural encoding*

The perception of objects and faces relies to some extent on different mechanisms and stimulus properties (e.g., Tanaka and Farah, 1993; for an overview see Bruce and Humphreys, 1994). In the literature different views regarding the underlying neural substrates of pictorial and structural encoding of faces and objects have been discussed (Chao et al., 1999; Haxby et al., 2001; Ishai et al., 2000; Kanwisher et al., 1997; McCarthy et al., 1997; Spiridon and Kanwisher, 2002).

Of interest for the issues here are ERP components that have been related to different stages of face and object processing. In this regard, the P100 is a positive-going deflection in the ERP with a peak latency of about 100 ms at occipital electrode sites and is thought to reflect early visual processes in extra-striate areas. It is sensitive to contrast, brightness, and size of a picture (Schendan et al., 1998). As yet there is little evidence that the P100 reflects face-specific processes (for an exception see Itier and Taylor, 2002, 2004a).

The subsequent N170 is a negativity around 150–200 ms at occipito-temporal sites that has been held to be face-specific (Bentin et al., 1996; Xu et al., 2005). However, several studies suggest that the N170 might not be face-specific but reflect the processing of fine-grained shape information for both face and non-face stimuli (e.g., Kiefer, 2001; Tanaka et al., 1999). Most of the pertinent studies failed to find familiarity effects (e.g., Eimer, 2000; Schweinberger et al., 2002a) or repetition effects in N170 (e.g., Eimer, 2000; Henson et al., 2004; Pfütze et al., 2002; Schweinberger et al., 1995; Tsivilis et al., 2001), suggesting that this component reflects structural encoding in general rather than recognition of individuals.

1.2. *Accessing stored structural representations*

Following perceptual encoding, models of face and object recognition posit the access to stored representations of both objects and faces. On the one hand, studies of brain damaged patients suggest the existence of double dissociations between face and object recognition (e.g., DeRenzi, 1986; McNeil and Warrington, 1993; Moscovitch et al., 1997). However, double dissociations do not necessarily indicate that the dissociated tasks are served by entirely independent modules because they might rely to a quantitatively different degree on the same mechanisms (Plaut, 1995) and may also depend on the categorization level and expertise of the patient (Gauthier et al., 1999).

On the other hand, there is an ongoing debate in the imaging literature whether familiarity of faces or objects activates category-specific regions in inferotemporal cortex such as the FFA. As reviewed by Henson et al. (2002) there are both positive and negative findings of familiarity effects in these regions. Even though, direct comparisons of familiarity effects for faces and non-face objects are relatively rare and not free of several interpretation problems. For instance, in the Gorno-Tempini and Price (2001) study the data indicate some category-specificity at a postperceptual level but they do not allow a distinction between the access to stored perceptual representations and semantic representations. In the study by Grill-Spector et al. (2004) the task for faces involved the identification of an individual face, whereas non-face discriminations (e.g., roses vs. other flowers) occurred at the subordinate level at best.

A further source of evidence about category specificity on a postperceptual level is the ERPs. In repetition priming Schweinberger et al. (1995) observed more negative ERP amplitudes for repeated relative to non-repeated faces over occipito-temporal regions and more positive amplitudes over fronto-central regions. This effect appeared rather early (around 250–300 ms) and was therefore termed early repetition effect (ERE) or – more recently – N250r. Several lines of evidence support the suggestion that the ERE/N250r reflects the access to domain-specific stored perceptual representations. The ERE/N250r is more pronounced for familiar than for unfamiliar persons (Herzmann et al., 2004; Pfütze et al., 2002; Schweinberger et al., 1995) and it is absent when faces are primed by portraits of different but semantically related persons (Lady Di → Prince Charles). In addition, when different portraits of the same person are presented as prime and target the ERE/250r is present, albeit smaller than when the same pictures are used (Schweinberger et al., 2002a). Brain electric source analysis (Schweinberger et al., 2002b, 2004) indicated a generator for the ERE/N250r in the fusiform gyrus, a region that has been found to be involved in face recognition (Kanwisher et al., 1997) and face repetition priming (Henson et al., 2000, 2002).

Two recent studies compared the ERE/N250r to faces and objects. In an immediate repetition paradigm Schweinberger et al. (2004) used pictures of faces and, among others, cars, an object category with perceptually homogeneous features. The authors observed an ERE/N250r for faces but not for cars. In a rapid-stream-stimulation paradigm Martín-Loeches et al. (2005) found ERE/N250rs to faces and names of famous persons and also to pictures of various common objects. The latter ERE/N250r, however, was markedly different in scalp topography from that to faces. Overall, these results seem to suggest different processes involved in accessing stored representations of faces and objects. However, in both studies the non-face objects were not accessed at exemplar level but at basic (Martín-Loeches et al., 2005) or subordinate level (Schweinberger et al., 2004). For that reason it remains unclear whether the findings of face-specific ERE/N250r relate to the different entry levels or to the different categorization processes performed on the stimuli. Therefore, it was the primary aim of the present study to compare faces and non-face objects that can likewise be accessed at the exemplar level in terms of their ERE/N250r.

1.3. *Accessing semantic memory*

The access to stored perceptual representations of familiar faces and objects is considered to be followed by the retrieval of semantic knowledge about the person or object. Studies with brain-damaged patients showing a selective loss of semantic knowledge in some but not other categories point towards category-specific knowledge stores (e.g., Caramazza and Mahon, 2003). Such dissociations also extend to knowledge about persons and knowledge about objects and animals (Thompson et al., 2004). Nevertheless, it is a much discussed issue whether such findings do in fact indicate category-specific semantic memory systems (for review, see Saffran and Sholl, 1999). Thus, accounts of distributed conceptual knowledge about different semantic categories within a unitary system (e.g., Tyler and Moss, 2001) contrast with notions that conceptual knowledge about different categories is represented in localizable multiple areas (e.g., Kiefer and Spitzer, 2001; Pulvermüller, 2001).

An ERP component possibly reflecting the access to semantic memory codes is the late repetition effect (LRE). The LRE was obtained with repetition and associative priming (Pfütze et al., 2002; Schweinberger, 1996; Schweinberger et al., 1995, 2002a), as enhanced positivity (or reduced negativity) at centro-parietal electrodes between 300 and 700 ms. These priming effects have been related to the N400 component, seen best when a word is presented out of a semantic context and therefore interpreted as reflecting retrieval from semantic memory (Kutas and Federmeier, 2000). In priming paradigms the N400 would be large for initial or unprimed presentations and diminished for repeated or primed presentations. The difference wave between primed and unprimed trials yields a late positive-going component, i.e., the LRE. Accordingly, LRE or N400 in face priming tasks might be related to the pre-activation of semantic knowledge about persons. This suggestion is supported by several lines of evidence. The LRE is similar to both faces and names of persons (Pfütze et al., 2002), it is modulated by face and name primes in a similar way (Schweinberger, 1996), and can be elicited also when faces are primed by portraits of semantically related but different persons (Schweinberger et al., 1995). Although it has been suggested that the LRE or N400 may be specific for stimulus categories (Kiefer, 2001, 2005; Sim and Kiefer, 2005; Kutas and Federmeier, 2000), to our knowledge there has as yet been no direct comparison between LRE/N400 to faces and other object categories. Therefore, it was the second aim of the present study to compare the LRE/N400 component elicited by faces and non-face objects in order to see whether person- and object-related knowledge would differ in terms of brain systems involved.

1.4. *The present study*

In the present study, the processing of familiar (at the exemplar level) and unfamiliar faces and buildings was compared by recording ERPs in a repetition priming paradigm (Fig. 1). The entry level was controlled by comparing faces of familiar persons (that is, individually nameable by the participants, e.g., Charlie Chaplin, Brad Pitt) with pictures of familiar buildings (likewise nameable, e.g., Brandenburg Gate, Sagrada Familia). The primes for the target faces and buildings could be either the same face or building (primed trials) or a different picture of the same category (unprimed trials). Participants had to decide for each target item whether it was familiar or unfamiliar.

Using different ERP components allowed us to compare face and object recognition at several levels, taking advantage of the temporal resolution of ERPs in two respects. For one, ERPs allow to distinguish several consecutive processes closely spaced in time and, second, the temporal variability of these various processes can be traced by ERP latency measurements. Both aspects can be used in assessing category-specific processing.

In line with previous research we expected that faces and buildings differ in the P100 and N170 to the extent that the images differ in basic visual properties and in their requirements for structural analysis. However, whereas intrinsic divergences in the visual properties of faces and buildings cannot be avoided, this is certainly not the case for subsequent processing stages. Accordingly, the main interest of the present study concerned the ERE/N250r and LRE components. If an ERE/N250r can be obtained also for objects, the scalp topographies of these repetition effects for faces and objects would indicate whether structural representations of faces and objects in memory are mediated by similar or different brain systems (McCarthy and Wood, 1985). Finally, to the extent that the LRE is an N400-like component and reflects the access to semantic

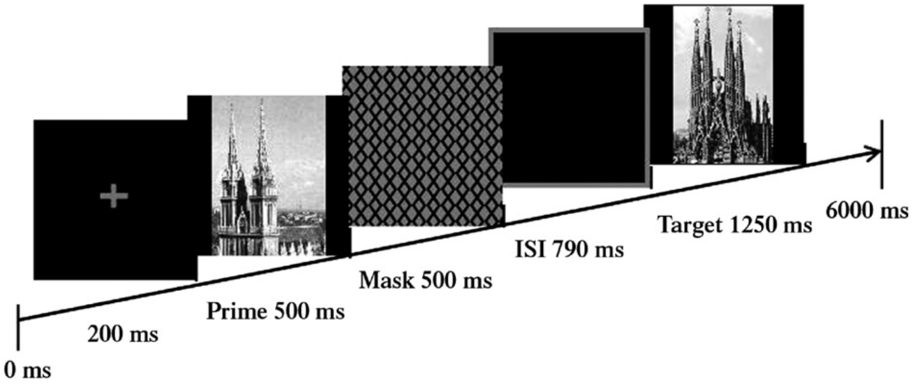

Fig. 1 – Example of trial sequence for an unprimed familiar building.

knowledge, it should elucidate the category specificity of semantic knowledge about persons and non-face objects.

2. Results

2.1. Performance results

Responses were scored as correct if the appropriate key was pressed within a time window from 100 to 2000 ms. Repeated measures ANOVAs were conducted on reaction time (RT) in correct trials to targets and percentage of errors (PE) with factors prime (primed, unprimed), category (faces, buildings) and familiarity (familiar, unfamiliar). Means and standard deviations of RTs are shown in Fig. 2.

As expected, RTs showed overall and strong effects of stimulus category, $F(1,15)=82.0$, $p<0.001$, familiarity, $F(1,15)=77.7$, $p<0.001$, and priming, $F(1,15)=299.9$, $p<0.001$. The priming effects were stronger for familiar than for unfamiliar items, $F(1,15)=56.3$, $p<0.01$, but – importantly – they were indistinguishable in magnitude for faces and buildings, $F(1,15)=1.1$, n.s. A three-way interaction of priming, familiarity and category emerged because there were stronger familiarity effects for buildings than for faces in the primed, $F(1,15)=23.4$, $p<0.1$, but not in the unprimed condition, $F(1,15)=5.3$, n.s. In addition, RTs for buildings showed a stronger familiarity effect than those for faces, $F(1,15)=15.1$, $p<0.1$.

In line with longer RTs for buildings than faces mean PE was noticeably higher for buildings, $F(1,15)=307.7$, $p<0.01$. Thus, relative to faces participants had more problems to judge the familiarity of buildings. A main effect of priming, $F(1,15)=8.6$, $p<0.1$, reflected the greater ease of familiarity decisions to primed relative to unprimed pictures of both categories.

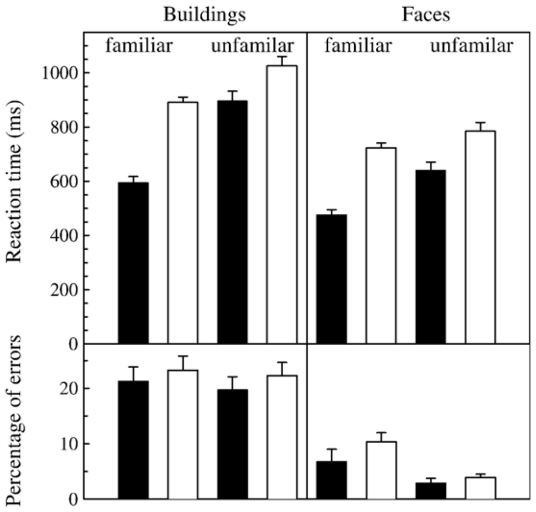

Fig. 2 – Means and standard errors of reaction times and percentage of errors to familiar and unfamiliar buildings (left) and faces (right). Black and white bars reflect responses to primed and unprimed stimuli, respectively.

2.2. Electrophysiological data

Fig. 3 shows ERP waveforms at selected electrode sites superimposed for familiar and unfamiliar faces and buildings and for primed and unprimed conditions. ERP deflections of primary interest here are the ERE/N250r and LRE, to be seen as differences between primed and unprimed conditions; in addition we also considered the P100 and N170 components.

2.2.1. P100

The P100 component at the occipital electrodes appears to be somewhat reduced for buildings than for faces but otherwise is little affected by experimental variables. P100 peak amplitudes and latencies were assessed in jackknifed grand averages (Miller et al., 1998). Measurement of ERP parameters in jackknife averages was first suggested for onsets of the lateralized readiness potential but is applicable also to other ERP parameters. Essentially, the grand average waveforms for each of the eight conditions were computed for subsamples including all participants except one, in the case of this study $16-1$ ($n-1$) participants. Then, parameters such as latencies and amplitudes are determined in the jackknife grand means and conventional statistics are performed on these parameters, controlling for the reduction of variance by correcting the F-values. The advantage of the jackknife procedure is a reduction of residual noise in the waveforms.

Electrode P10 was used for the determination of latencies. ANOVA of peak amplitudes confirmed a main effect of stimulus category, $F(59,885)=2.7$, $p<0.01$, with P100 to buildings being smaller than to faces (6.0 and 7.0 μV, respectively, at electrode O2). A main effect of category was also found for P100 latency, $F(1,15)=7.2$, $p<0.5$, which was longer for buildings than for faces by about 10 ms.

2.2.2. N170

This component was most pronounced at occipito-temporal electrodes PO10 and PO9 and was larger for faces than buildings. The insert of Fig. 3 also indicates possible modulations by familiarity at least for faces. Average N170 amplitude was determined in a time segment between 150 and 200 ms, which covers its peak for both stimulus categories. Confirming the visual impression there was a strong category effect, $F(59,885)=30.7$, $p<0.01$, and a main effect of familiarity, $F(59,885)=3.2$, $p<0.1$. No effect of priming could be found, $F(59,885)=1.2$, n.s.

For a closer inspection of N170 amplitudes and latencies, peaks were determined in jackknifed grand averages. Analysis of peak amplitudes confirmed both the category effect, $F(59,885)=20.5$, $p<0.01$, and the familiarity effect, $F(59,885)=2.2$, $p<0.01$. To further elucidate these results, a region of interest was defined at posterior electrodes (P7, P8, P9, P10, PO7, PO8, PO9, PO10) where N170 to faces was largest (see Fig. 3). Results confirmed the category effect, $F(7,105)=4.4$, $p<0.01$. No main effect of familiarity was present, $F<1$, but familiarity significantly interacted with category, $F(7,105)=2.3$, $p<0.5$. Post hoc analysis revealed that this interaction is due to a trend for a familiarity effect for faces, $F(7,105)=2.2$, $p=0.8$, with familiar faces eliciting slightly

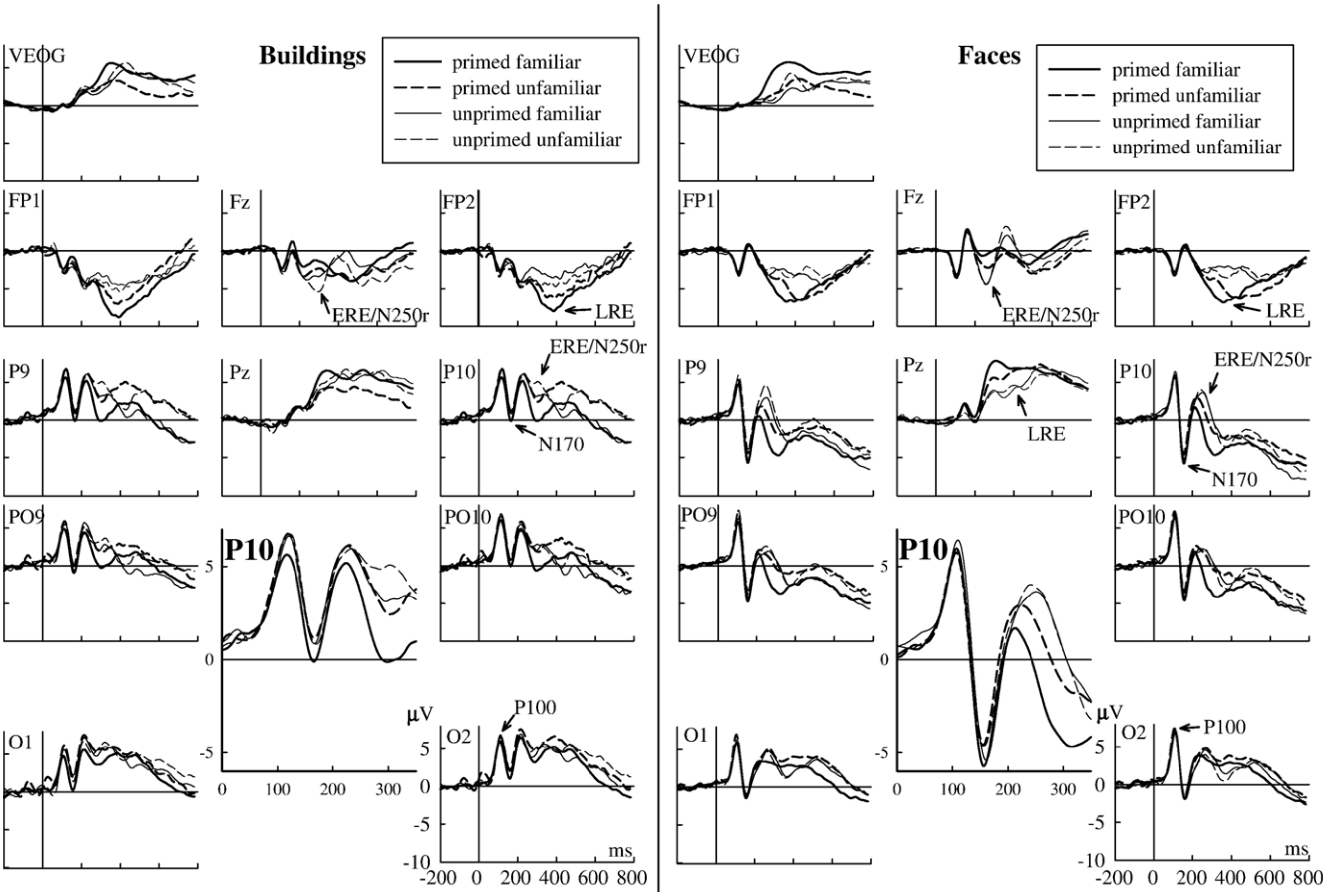

Fig. 3 – ERP waveforms at selected electrode sites and vertical electrooculogram (VEOG) for faces (right) and buildings (left), superimposed for familiar and unfamiliar, primed and unprimed stimuli. Arrows are pointing to ERP components of primary interest: the P100 and N170, and the repetition effects between about 260 and 340 ms (ERE/N250r) and 400 to 500 ms (LRE), to be seen as differences between primed and unprimed conditions. The inserts show magnifications of the P10 electrode, allowing a better view of experimental effects on the P100, N170 and ERE/N250r components.

larger N170s than unfamiliar faces, but not to buildings, $F<1$. The N170 latencies differed significantly for both categories, $F(1,15)=6.3$, $p<0.5$, being longer for buildings than for faces by about 10 ms.

2.2.3. ERE/N250r

In Fig. 3 the ERE/N250r can be seen during a 260- to 340-ms time segment for both stimulus categories with the primed condition being less negative (or more positive) than the unprimed condition at frontal electrodes and more negative at occipito-temporal electrodes. The ERE/N250r is highlighted in the difference waves (primed–unprimed), depicted in Fig. 4.

The ERE/N250r was quantified as average amplitude in the time segment 260–340 ms. ANOVA confirmed the priming effect, $F(59,885)=13.5$, $p<0.01$, which – importantly – was present not only for faces, $F(59,885)=13.6$, $p<001$, but also for buildings, $F(59,885)=6.8$, $p<0.01$, when each category was tested alone. The ERE/N250r was larger for faces than buildings as reflected in a Priming×Category interaction, $F(59,885)=2.6$, $p<0.5$. The priming effect interacted also with familiarity, $F(59,885)=8.3$, $p<0.01$, because ERE/N250r was present only for familiar, $F(59,885)=19.6$, $p<0.01$, but not for unfamiliar items, $F(59,885)=1.9$, n.s. In addition, there were main effects of category, $F(59,885)=8.0$, $p<0.01$, and familiarity, $F(59,885)=8.1$, $p<0.01$, due to larger ERP amplitudes both into positive- and negative-going directions for faces compared to buildings and for familiar items compared to unfamiliar items, respectively.

In order to check whether the effects in the area measures are independent of latency differences between categories, the priming effects for the two conditions were extracted by subtracting unprimed from primed trials (Fig. 4). In line with previous reports, the ERE/N250r showed up in difference waves in an occipito-temporal negativity and a fronto-central positivity. Peak amplitudes and latencies were determined in jackknifed averages of these difference waves. Although the ERE/N250r was not significant for unfamiliar items in the area measures, there was a recognizable peak for these items in the jackknifed grand means. The peak latency, determined at the P10 electrode, was later by about 30 ms for buildings than for faces, $F(1,15)=7.5$, $p<0.5$. ANOVAs of peak amplitudes of the ERE/N250r mostly confirmed the results for the area measures. A familiarity effect was found, $F(59,885)=4.0$, $p<0.01$, because ERE/N250r was much larger for familiar than for unfamiliar items. The

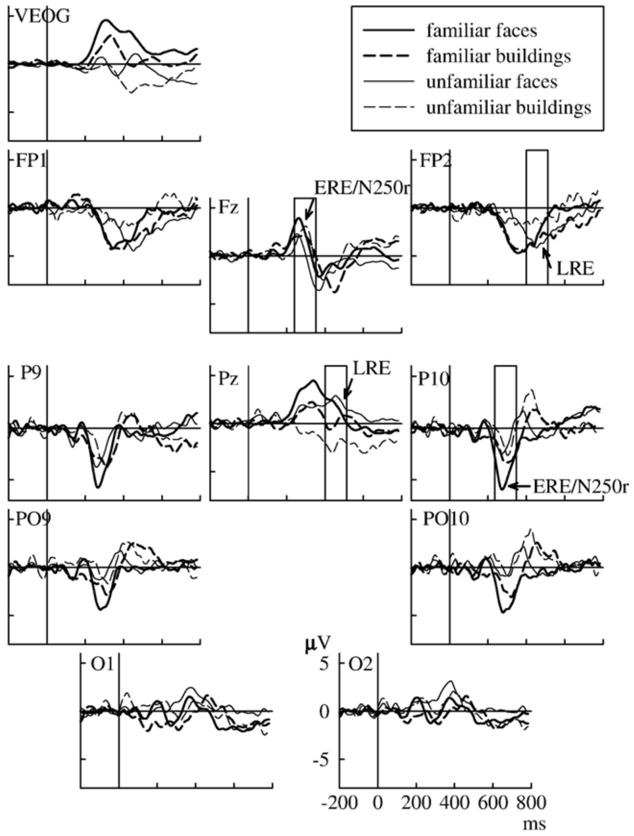

Fig. 4 – Difference waves (primed-unprimed) for familiar and unfamiliar faces and buildings at selected electrodes and vertical electrooculogram (VEOG), highlighting the repetition effects between about 260 and 340 ms (ERE/N250r) and 400 to 500 ms (LRE) with vertical boxes.

amplitude of the priming effect for faces and buildings differed only as a trend, $F(59,885)=1.3$, $p=0.8$.

Because in the overall ANOVA the ERE/N250rs for faces and buildings differed in interaction with electrode it is of interest whether this is merely due to differences in signal strength or also in scalp distribution. The top panel of Fig. 5 shows the scalp distribution of the mean amplitudes of ERE/N250r difference waves in the 260- to 340-ms time segment, which does not seem to indicate any differences apart from those in overall amplitude. The topographies of these ERE/N250r amplitude measures were assessed by ANOVAs following normalizing them with the vector method (McCarthy and Wood, 1985). Please note that such an analysis was not feasible for peak amplitudes because those had been derived from jackknifed grand means. Because there had been no priming effect for unfamiliar targets in the ANOVA of mean amplitude measurements the topography of the priming effect was only compared for familiar targets in the two categories. This comparison showed no significant differences in the topographies for both categories, $F<1$.

Summarizing, an ERE/N250r component could be obtained for both familiar faces and familiar buildings. In addition, the topographies and, consequently, the involved neural generators, were indistinguishable between faces and buildings.

2.2.4. *LRE/N400*

As can be seen in Figs. 3 and 4 priming effects were also present beyond the ERE/N250r interval. For faces, this late repetition effect consisted in increased positivities for primed relative to unprimed faces at centro-parietal electrodes and increased negativities at prefrontal electrodes. This is in line with previous reports. For buildings there were also LREs but with a quite different scalp topography than for the faces, as can be seen in the distributions of the difference waves between 400 and 500 ms (Fig. 5).

The LREs were first analyzed in consecutive 50-ms time segments between 350 and 750 ms. Priming effects were found from 350 to 500 ms, but not thereafter. Furthermore, no prime by familiarity interaction was found after 400 ms, which distinguishes these late priming effects from the ERE.

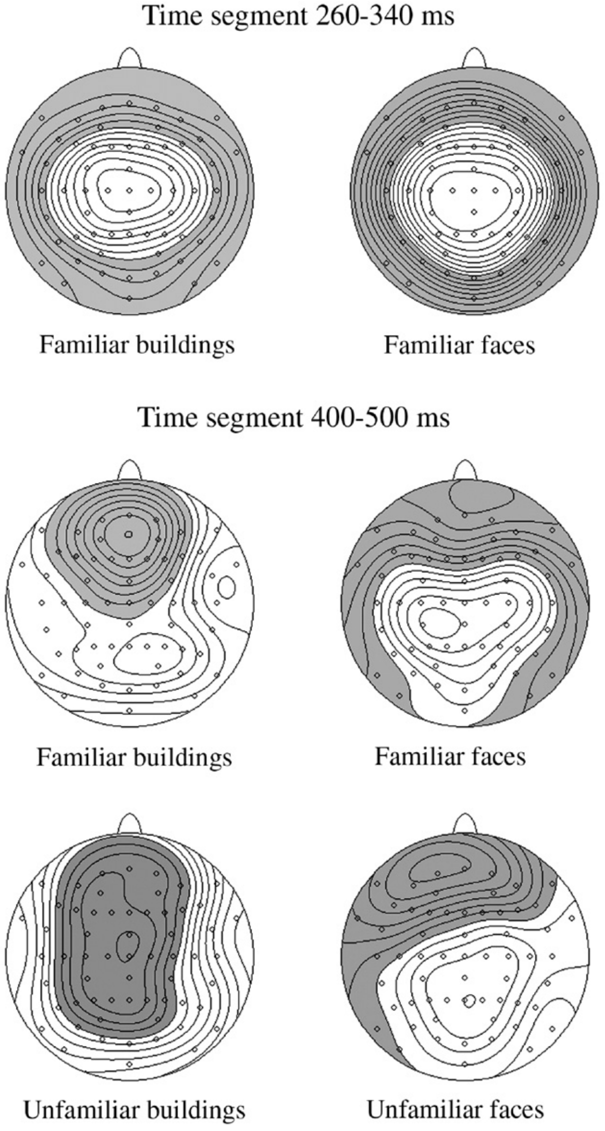

Fig. 5 – Scalp topographies of difference waves. Top: ERE/N250r in the time segment 260–340 ms for familiar faces (right) and buildings (left). Bottom: LRE in the time segment 400–500 ms for familiar and unfamiliar faces (right) and buildings (left). The gray areas correspond to negative voltages; isopotential lines represent steps of 0.67 μV.

Therefore, the following analyses focused on the 400- to 500-ms interval. All conditions showed significant effects in interaction with factor electrode: category, $F(59{,}885)=10.2$, $p<0.01$, familiarity, $F(59{,}885)=3.1$, $p<0.5$, and prime, $F(59{,}885)=5.4$, $p<0.1$. Importantly, there was also an interaction between category and prime, $F(59{,}885)=7.1$, $p<0.01$. Analysis of topographies with vector-scaled data revealed a strong category effect, $F(59{,}885)=7.2$, $p<0.01$. Therefore, the LRE to faces and buildings are qualitatively different, with LRE to faces being characterized by a parietal positivity and for buildings by a frontal negativity.

3. Discussion

This study investigated the category specificity of face and object recognition when both processes involve individual exemplars of a category. The main instrument of research was several components of the event-related brain potential with a focus on the early and the late repetition effects (ERE/N250r and LRE). Both components are characterized by their modulation due to the repetition of the eliciting stimulus. The results indicate that the ERE/N250r may be less specific for faces as has been previously thought, whereas the observed LRE appears to be sensitive for the stimulus category.

Responses to buildings took longer and were more error prone than responses to faces. Interestingly, this difference in recognition performance occurred despite similar pre-experimental familiarity ratings on the basis of the name lists for those faces and buildings that had been individually selected for each participant. Likely, name-based familiarity ratings and recognition performance of the pictorial representation of the item only tap partially overlapping aspects of memory.

As expected, RTs were shorter and more accurate to primed than to unprimed stimuli. Importantly, these priming effects were independent of the stimulus category and of the overall differences in recognition performance. In line with previous reports (e.g., Herzmann et al., 2004; Schweinberger et al., 1995) the priming effect in RTs interacted with familiarity, benefits being larger from priming for familiar than for unfamiliar items. This effect is suggested to indicate that apart from perceptual processes repetition priming also affects subsequent identity-related recognition, that is, the access to FRUs and ORUs in the models of Bruce and Young (1986) and Ellis and Young (1996), respectively.

3.1. *Pictorial and structural encoding*

Perceptual processes were assessed by measuring the P100 and N170 components. P100 amplitude was smaller for buildings than for faces. In principle the P100 amplitude might reflect differences in the mechanisms underlying early visual processing of buildings compared to faces, such as the degree of holistic processing for faces as compared to buildings (cf., Itier and Taylor, 2002, 2004a). However, because there were also a number of unavoidable low level visual differences between the faces and the buildings in the present study, such as spatial frequency content, height to width ratio, or contrast, the category differences in P100 amplitude observed here may also relate to such factors. In the same line, one could interpret the observed 10-ms delay in P100 latency to buildings as compared to faces to be consequence of differences in low-level visual processes.

The 10-ms delay in the N170 might be a mere propagation of the delay in the P100 and need not be attributed to any additional processing difficulties during structural analysis. N170 amplitude showed a pronounced category effect and was very small for buildings. This is in line with findings that are suggestive of face specificity of the N170 (Bentin et al., 1996; Itier and Taylor, 2004b). The present findings might be seen at variance with reports that N170 may occur also to other stimuli for which there is expertise (e.g., Rossion et al., 2002). One should keep in mind, however, that the kind of expertise that induces non-face N170 responses may be different from the kind of expertise required to recognize visually diverse buildings.

3.2. *Accessing stored structural representations*

In the present study the entry level was controlled in requiring familiarity classifications of faces and buildings that were both identifiable as exemplars. Any differences in the ERE/N250r, presumably reflecting the access to stored structural representations, might therefore be attributed to the stimulus category. In contrast to the studies of Martín-Loeches et al. (2005) and Schweinberger et al. (2004), we observed clear ERE/N250r components to non-face objects that in crucial respects were similar to the ERE/N250r in response to faces. However, there were also some differences, which shall be discussed first.

Although present for familiar buildings, the ERE/N250r to familiar faces was both larger and earlier. This does not necessarily imply face specificity of this component because the ERE/N250r can be quite variable also for faces. Thus, Herzmann et al. (2004) found larger ERE/N250rs for personally familiar than for familiar faces and the reported peak latency varies between 250 ms (Schweinberger et al., 1995) and 300 ms (Pfütze et al., 2002). Therefore, the differences in amplitude and latency between the ERE/N250r for faces and buildings might relate to the better structural representation of the familiar faces in memory as was also reflected in the shorter RTs and lower error rates for these stimuli.

More relevant for the question of category specificity than amplitude and latency differences are the scalp topographies and effects of experimental variables. The comparison of the scalp distributions of the ERE/N250r of familiar faces and familiar buildings showed no significant differences. Therefore, the underlying source contributions to the ERE/N250r in both categories, faces and buildings, appear indistinguishable. This finding is in contrast to the demonstration of domain specificity of the ERE/N250r regarding pictures and names by Pfütze et al. (2002). These authors suggested that whereas the ERE/N250r to faces reflects the strengthening of links between FRUs and PINs, the ERE/N250r for names reflects the strengthening of links between name recognition units and PINs. Along this line of reasoning, the indistinguishable ERE/N250rs to faces and buildings may indicate that the cognitive architecture for the individually identifiable stimuli may be very similar, possibly involving a common system of recognition units and/or their links to identity nodes.

For both stimulus categories, the ERE/N250r was modulated by stimulus familiarity in that it was present only to familiar items but absent or at least very small to unfamiliar items. This kind of familiarity dependency of the ERE/N250r is very typical for this component and has always been found when the relevant comparison has been made. It is also a major argument for the sensitivity of this component for the existence of representations of the eliciting stimuli in memory (Bruce and Young, 1986; Pfütze et al., 2002; Schweinberger et al., 1995). Importantly, the current findings provide evidence that the ERE/N250r does not only reflect stimulus-triggered access to stored facial representations but also to stored representations of buildings.

3.3. *Semantic memory*

The second main issue of the present paper concerned the late repetition effect (LRE), a component presumably reflecting the access to semantic memory. For faces, the LRE observed here resembles previous results (Bentin and McCarthy, 1994; Paller et al., 2003; Pfütze et al., 2002; Schweinberger et al., 1995) that have been interpreted as reflecting variations of an N400 component (Bentin and McCarthy, 1994; Schweinberger, 1996).

For buildings we also obtained a sizeable LRE. However, the scalp topography of the LREs for buildings markedly differed from that for faces. Such differences are not unprecedented. Kiefer (2005) also reported differential priming effects to natural and artifactual (e.g., animals vs. tools) categories in a late time window between 300 and 500 ms. If the LRE does reflect the access to semantic knowledge, the present findings are clearly at variance with the idea of a unitary, category-independent semantic knowledge store (Tyler and Moss, 2001). It is in line, however, with suggestions about category-specific semantic representations, which may be related to particular kinds of information localized in different regions of the cerebral cortex (Hinojosa et al., 2001; Saffran and Sholl, 1999). In the present case, one would have to assume differences between knowledge about persons and buildings, somehow mapping onto different brain systems. It has been argued that knowledge is stored in those brain areas that are responsible for processing relevant aspects of the events in question. For example, knowledge about animals would involve mainly perceptual aspects, whereas knowledge about tools would involve predominantly knowledge about actions, leading to differential contributions of sensory and motor cortices when these representations are activated (Kiefer, 2001; Kiefer and Spitzer, 2001; Pulvermüller, 2001). According to the present results semantic knowledge about persons and buildings appears to involve partially non-overlapping brain areas.

In order to specify what precisely the differences in person- and building-related knowledge might be, there is a problem, namely that – in line with other reports (e.g., Pfütze et al., 2002; Schweinberger et al., 1995) – the LRE was of similar magnitude and topography for familiar and unfamiliar items. Therefore it is difficult to argue that the LRE reflects the specific knowledge about an individual person or building. In that case the LRE should be larger for familiar than unfamiliar items. Alternatively, the LRE might reflect the access to some generic kind of knowledge about persons or buildings in general. The access to that kind of knowledge would then be facilitated by repetition priming. On the other hand, there have also been reports of LRE-like associative priming effects for related as compared to unrelated persons (Schweinberger, 1996; Schweinberger et al., 1995). Although these associative priming-related LREs are usually considerably smaller than those based on repetition priming, they indicate a possible specific knowledge contribution to the LRE. Nevertheless, the usually sizeable LREs also for unfamiliar persons indicate that the generic aspects dominate.

Then, what could be the basic difference in knowledge about persons and buildings? One suggestion would follow the idea that there are different kinds of ontological categories or concepts for different types of objects (e.g., Boyer, 2003). Thus the concept of a person would involve such notions as natural object, living being, eats, drinks, procreates, has intentions, moves about etc., whereas buildings are man-made objects build from stone or other non-living material, are immobile, serve certain purposes, etc. These properties hold for any person or building, respectively, be they familiar or unfamiliar. Because the person and building concepts involve very different elements it is plausible that also the brain systems responsible for such elements may differ; hence the facilitation of these systems by priming would be category-, or concept-specific. Whatever the case, the present results about the LRE show for the first time that semantic knowledge about persons and similarly unique non-face objects have separate representations in the brain. Future studies might attempt a more precise localization of these representations and extend this technique to other knowledge categories.

3.4. *Conclusion*

In conclusion, by controlling for the entry level at individual exemplars we have for the first time been able to demonstrate an ERE/N250r component for non-face objects (buildings), presumably indicating the access to structural representations stored in memory. For famous faces and buildings these processes appear to rely on similar or at least closely neighbored brain systems. In addition, we showed that the LRE/N400 to famous faces and buildings, closely following the ERE/N250r in time, displays a very distinct category-specific scalp topography. This supports the idea that semantic knowledge about these object categories relies on at least partially non overlapping brain systems. Together with the stimulus-specific effects on the earlier P100 and N170 components, reflecting lower level perceptual and structural analyses, the present data about the later memory-related processes extend our knowledge about the levels at which category-specific processes may occur.

4. Experimental procedures

4.1. *Participants*

The experiment involved 16 participants (10 female). Seven further participants had been excluded due to technical problems, excessive artefacts or high error rates while discriminating familiar and unfamiliar buildings (percentage of hits minus false alarms <40%). Mean age of participants was 25.6 years (range: 21–37). The Edinburgh Handedness Inventory (Oldfield, 1971) indicated that most participants were right-handed; one was ambidextrous (mean handedness score = 75.01, range: 9.1–100). Participants were students and German residents, reported normal or corrected-to-normal visual acuity, and were reimbursed for attendance.

4.2. *Stimuli and apparatus*

Two sets of black and white pictures were used, consisting of 128 portraits and 128 photos of buildings each, all background being removed. Pictures in each set were, in equal parts, familiar and unfamiliar to the participants. This was achieved by selecting the familiar items individually for each participant. One week before the experiment participants completed a questionnaire consisting of the names of 104 famous buildings and 104 famous persons plus 2 foils each. Participants rated on four-point scales how likely he or she would recognize this building/face when seeing its picture/portrait. Only participants with sufficient knowledge of both, familiar faces and buildings, were accepted for the study. For each accepted participant 64 items from each category with the highest ratings were selected as familiar stimuli to be used in the experiment. Mean ratings of familiarity for the selected items were 3.81 (SD = 0.16) and 3.68 (SD = 0.23) for faces and buildings, respectively. Portraits of familiar and unfamiliar persons were fit within black frames of 105 × 125 pixels (3.7 by 4.4 cm) corresponding to visual angles of 2.65 by 3.16° at the viewing distance of 80 cm. The unfamiliar faces were matched to familiar ones with respect to gender, approximate age and general portrait style. Pictures of buildings were collected from the Internet and edited with Adobe Photoshop™ to a unitary format. Unfamiliar buildings were matched to familiar ones as to architectural style, epoch, and type of building such as churches, towers, or monuments. All photos of buildings were inserted into an area of 125 × 125 pixels (4.4 × 4.4 cm), corresponding to visual angles of 3.16°. Naturally, pictures of buildings were more variable in their height to width ratio than portraits. Mean luminance of faces and buildings was 43.8 lx (SD = 13.1) and 49.1 (SD = 15.4), respectively. In addition to faces and buildings two masks were created, corresponding in size to the pictures of faces and buildings, respectively. The masks consisted of a grey background, covered with a black cross-hatched pattern (cf., Fig. 1).

4.3. *Procedure*

Participants were seated in a dimly lit, sound-attenuated and electrically shielded room. After application of the electrodes participants received written task instructions. Sixteen practice trials consisting of eight trials each with spare faces and buildings were followed by the experimental trial blocks. The practice trials were repeated after the first half of the experiment when response key assignments were switched. Pictures were presented in the centre of a black CRT monitor (Mitsubishi Diamond Pro 920) with a resolution of 640 by 480 pixels.

The trial scheme is shown in Fig. 1. Each trial started with a fixation cross replaced after 200 ms by a prime, displayed for 500 ms. Then, a mask was shown for 500 ms, followed for 790 ms by a black frame of the same size as the following picture. Thereafter the target item was presented for 1250 ms. Between target offset and the next trial, the screen remained blank for 2760 ms.

Each of the eight experimental blocks consisted of 32 trials. Blocks were separated by short breaks and consisted either of faces or buildings and alternated between these conditions. The starting condition was balanced across participants. Participants had to decide for each target item whether it was familiar or unfamiliar by pressing one of two buttons with the right or left index finger. The response key assignment to familiar and unfamiliar responses was reversed after four blocks with initial assignment being balanced across participants. Both, speed and accuracy of responses were emphasized. The primes for the target faces and buildings could be either the same face or building (primed trials) or a different picture of the same category (unprimed trials). In the unprimed trials the preceding prime for a familiar target was always an unfamiliar item, and unfamiliar targets were always preceded by familiar items. This appeared to be justified because previous work had shown that ERPs to unprimed faces is unaffected by prime familiarity (Schweinberger et al., 1995). Each target item was presented twice but in different halves of the experiment, separated by at least 15 min and 100 intervening items, a condition that abolishes the ERE/N250r to faces (Schweinberger et al., 2002a).

4.4. *ERP recording*

The electroencephalogram (EEG) was recorded from 62 tin electrodes mounted in an electrode cap (Easy-Cap™) at positions FPz, FP1, Fp2, AF3, AF7, AF4, AF8, Fz, F1, F3, F5, F7, F9, F2, F4, F6, F8, F10, FCz, FC3, FT7, FT9, FC4, FT8, FT10, Cz, C1, C3, C5, T7, C2, C4, C6, T8, CPz, CP3, TP7, TP9, CP4, TP8, TP10, Pz, P1, P3, P5, P7, P9, P2, P4, P6, P8, P10, PO3, PO7, PO9, PO4, PO8, PO10, Oz, O1, O2, and Iz (Pivik et al., 1993). The average of TP9 and TP10 electrodes served as initial common reference, and a forehead electrode served as ground. Additional electrodes were placed above the left and right eye, to record the vertical electrooculogram (EOG); the horizontal EOG was measured with electrodes F9 and F10. Electrode impedance was kept below 5 kΩ. Offline the EEG was recalculated to average reference. All electrical signals were amplified with Brain Amps amplifiers and continuously recorded with a sampling rate of 250 Hz and a band-pass of 0.03 to 70 Hz.

4.5. *Data analysis*

Offline the continuous EEG was segmented into 1-s epochs starting 200 ms before target onset and averaged separately for each channel and experimental condition. Only trials with correct responses and without artefacts were analyzed. ERPs were aligned to a 200-ms baseline before target-onset and digitally low-pass filtered at 10 Hz (12 db/octave). ERPs were quantified by peak amplitude and latency and mean amplitude measures and were submitted to ANOVAs with repeated measurements on category, priming, familiarity, and, when appropriate, electrode site. The Huynh–Feldt correction was applied to all ANOVAs. When indicated by significant interactions, post hoc analyses were performed with the Bonferoni correction. Results are presented with uncorrected degrees of freedom and the corrected *p*-value. Because the average reference sets the mean activity across all electrodes to zero, condition effects in ANOVAs with all electrodes are only meaningful in interaction with electrode. Therefore, in those analyses the factor electrode will not be mentioned for brevity's sake.

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