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## Research Report

# Early electrophysiological correlates of adaptation to personally familiar and unfamiliar faces across viewpoint changes

Stéphanie Caharel<sup>a,b</sup>, Corentin Jacques<sup>b,c</sup>, Olivier d'Arripe<sup>b</sup>,  
Meike Ramon<sup>b</sup>, Bruno Rossion<sup>b,\*</sup>

<sup>a</sup>Laboratoire Interpsy, psychologie de l'interaction et des relations intersubjectives, Nancy Université (Nancy 2), France

<sup>b</sup>Institute of Research in Psychology and Institute of Neuroscience, Université Catholique de Louvain, Belgium

<sup>c</sup>Stanford University, Department of Psychology and Neuroscience Institute, USA

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## ABSTRACT

Behavioral studies have shown that matching individual faces across depth rotation is easier and faster for familiar than unfamiliar faces. Here we used event-related potentials (ERPs) to clarify the locus of this behavioral facilitation, that is whether it reflects changes at the level of perceptual face encoding, or rather at later stages of processing. We used an identity adaptation paradigm in ERPs, during which a first (adapting) face (~3000 ms) rotated 30° in depth was followed by a second full front face (200 ms) which was either the same or a different identity as the first face. For unfamiliar faces, the early face-sensitive N170 component was reduced for immediately repeated as compared to different unfamiliar faces in the right hemisphere only. However, for personally familiar faces, the effect was absent at right hemisphere electrode sites and appeared instead over the left hemisphere at the same latency. Later effects of face identity adaptation were also present on the scalp, but from about 300 to 400 ms over fronto-central regions, and slightly later on occipito-temporal regions, there was a strong adaptation effect only for familiar faces. These observations suggest that the perceptual encoding of familiar and unfamiliar faces may be of different nature, as indicated by early (N170) hemispheric differences for identity adaptation effects depending on long-term familiarity. However, the behavioral advantage provided by familiarity to match faces across viewpoints might rather be related to processes that are closer in time to the behavioral response, such as semantic associations between the faces to match.

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## 1. Introduction

Associating two different views of the same unfamiliar person's face may be quite difficult, but familiarity with faces can make this task extremely easy (Bruce, 1982; Bruce et al., 1999; Hancock

et al., 2000; Hill et al., 1997; O'Toole et al., 1998; Young et al., 1986). However, the mechanisms by which familiarity enhances the ability to match distinct face pictures of the same person (or discriminate facial pictures belonging to different persons) remain largely unclear. On the one hand, it may be that this

\* Corresponding author at: Institute of Research in Psychology, Université Catholique de Louvain, 10 Place du Cardinal Mercier, 1348 Louvain-la-Neuve, Belgium. Fax: +32 10 47 37 74.

E-mail address: [bruno.rossion@uclouvain.be](mailto:bruno.rossion@uclouvain.be) (B. Rossion).

facilitation is caused indirectly, at a relatively late stage of processing. For instance, when matching two pictures of the same person's face, each derived face representation may activate the same semantic and lexical information (i.e., the person's occupation, name), leading to an indirect reinforced association between the two facial images. In this situation, people may also be more confident about their decision of matching or discriminating individual faces, and thus decisional factors may contribute to the advantage found for familiar over unfamiliar faces. On the other hand, and more interestingly, familiarity may also change the nature of facial representations such that the association between different pictures of the same person may be reinforced already at the perceptual level when faces become familiar. The classical view of the unfolding of face processing stages rather supports the first view. For instance, in the influential face processing model of [Bruce and Young \(1986\)](#), the structural encoding stage, namely a stage that captures those aspects of the structure of a face essential to distinguish it from other faces, is not influenced by familiarity of the face input. The structural encoding stage might contain viewpoint-independent or viewpoint-dependent codes (see [Bruce and Young, 1986](#)), but familiarity of the face is not thought to have an influence at this level, which precedes and lead to the activation of long term familiar recognition units (FRUs).

While it is difficult to address this question by means of behavioral investigations alone, fMRI (functional Magnetic Resonance Imaging) studies indicate that matching of faces across viewpoint is modulated by familiarity in the human brain. For example, a study found that repetition of unfamiliar faces across different views produced repetition decreases in a medial portion of the right fusiform gyrus, whereas the same effect for familiar faces was rather found in left middle temporal and left inferior frontal cortices ([Pourtois et al., 2005a](#)). These results suggest that recognition of familiar faces may involve higher-level semantic systems in the temporo-frontal cortex rather than the perceptual systems in the fusiform gyrus, in line with an influential neuro-functional architecture of face processing ([Haxby et al., 2000](#); [Gobbini and Haxby, 2007](#)). In contrast to these observations, [Eger et al. \(2005\)](#) found an increasing degree of generalization over image changes from mid- to anterior face-responsive regions in the fusiform gyrus, only for familiar faces, a result that would rather suggest that familiarity modulates earlier steps (i.e., perceptual) face matching. This latter observation is also in agreement with findings from positron emission tomography (PET) studies that, independently of viewpoint variations, visually familiar faces activate face-sensitive and more general right hemisphere occipito-temporal areas to a lesser extent than unfamiliar faces ([Rossion et al., 2001; 2003](#); for fMRI evidence, see [Gobbini and Haxby, 2006](#)). However, while PET or fMRI is useful to disclose the localization of such effects in the human brain, the low-temporal resolution of these methods is of little help if one aims at clarifying the temporal locus of the influence (i.e., facilitation) on the ability to match different face views by long-term familiarity.

Because of their high temporal resolution, methods such as event-related potentials (ERPs) recorded from the human scalp are better suited to address this issue. Presentation of a face stimulus generally leads to a sequence of visual ERPs,

the most prominent being the occipito-temporal N1 peaking at about 170 ms following face onset, and termed the N170 ([Bentin et al., 1996](#); for early studies see also [Jeffreys, 1989](#); [Bötzel et al., 1995](#); [George et al., 1996](#); for a recent review see [Rossion and Jacques, 2011](#)). The N170 is of particular interest for researchers aiming at understanding the time-course of face processing since its onset (120–130 ms) marks the first face-sensitive response that cannot be accounted for by low-level visual cues (e.g., spatial frequencies, color; [Rousselet et al., 2005](#); [Rossion and Caharel, in press](#)) and the N170 component shows a consistent larger amplitude to faces than other objects categories ([Rossion and Jacques, 2008](#)).

Interestingly, many studies have shown that the amplitude of the N170 (or the M170 in magnetoencephalography, MEG) is reduced in response to an immediately repeated individual face stimulus as compared to the response to an unrepeatd face stimulus ([Caharel et al., 2009a; 2009b](#); [Campanella et al., 2002](#); [Ewbank et al., 2008](#); [Guillaume and Tiberghien, 2001](#); [Heisz et al., 2006](#); [Itier and Taylor, 2002, 2004](#); [Jacques et al., 2007](#); [Jacques and Rossion, 2009](#); [Kuefner et al., 2010](#); [Martens et al., 2006](#)). This effect emerges at around the peak of the component (160–170 ms) and cannot be accounted for by low-level visual cues, given its absence when the same face stimuli are presented upside-down ([Jacques et al., 2007](#)). These observations suggest that individual unfamiliar faces can be discriminated/matched as early as 160 ms in the occipito-temporal cortex.<sup>1</sup>

Recently, it has been shown that the amplitude difference at the level of the N170 for immediately repeated vs. unrepeatd unfamiliar faces can be observed despite substantial changes of viewpoint (30°) between the two faces presented ([Caharel et al., 2009a](#)). This latter observation indicates that the matching of individual unfamiliar faces across viewpoint changes is initiated as early as the first perceptual encoding of a face, as indexed by the N170 ([Rossion and Jacques, 2011](#)).

Considering this evidence, the present study aimed at testing whether long-term familiarity with faces may modulate this early identity-adaptation effect. On the one hand, modulation of the N170 identity-adaptation effect across viewpoint changes by long-term face familiarity would support the view that perceptual encoding of familiar and unfamiliar faces differ, offering an explanation why familiar faces are matched more easily across different viewing conditions than unfamiliar faces. However, on the other hand, finding that the behavioral facilitation by familiarity is not associated with a modulation of this early effect but rather with modulations at a later time course during the processing of faces would rather suggest that familiar and unfamiliar faces are perceptually encoded in the same way, and that

<sup>1</sup> In a few ERP studies, mainly performed by [Schweinberger and colleagues \(2002a, 2002b\)](#), the N170 amplitude did not differ significantly between immediately repeated and unrepeatd faces. However, the focus of these studies was not on the N170, which was not analyzed in depth by considering specific electrodes of interest, but rather on later components in a lower frequency range. Probably for this reason, the EEG data was severely low-pass filtered (<10 Hz), reducing the sensitivity of the N170, a component associated with an increase of power between 5 and 15 Hz (e.g., [Rousselet et al., 2007](#)).

other factors (semantic, lexical, decisional, ...) explain the behavioral advantage at matching faces presented under different viewpoints.

To disentangle these two possibilities, we used a face identity adaptation paradigm across viewpoint changes as in Caharel et al. (2009a) (Fig. 1), this time familiar faces in addition to unfamiliar faces. Also, in contrast to most behavioral and neuroimaging studies that compared the processing of unfamiliar and familiar faces using the photographs of famous people, we used personally familiar faces. Indeed, faces of people frequently encountered in real-life under a variety of viewing conditions such as changes in viewpoint, lighting, and expression, leads to particularly robust face representations (Carbon, 2008; Herzmann et al., 2004; Tong and Nakayama, 1999). Here, one of the groups of participants to the study was from the same classroom. They were personally familiar with half of the face photographs presented during the experiment, as they had been in the same classroom as the people whose faces were used as the familiar set for at least a year-and-a-half at the time of testing. Thus, they had extensive long-term visual experience experience with these faces.

## 2. Results

Two groups of participants, one personally familiar with half of faces (“familiar” group) and the other one unfamiliar with all faces (“unfamiliar” group), were tested in this experiment. During an identity adaptation paradigm, participants were presented first with an adapting face stimulus (~3000 ms) rotated 30° in depth, followed by a second face (200 ms) from a frontal view of either the same or a different identity (Fig. 1). Participants performed an individual face matching task, comparing the identity of adapting and test faces.

### 2.1. Behavioral data

Analyses revealed significant interactions between the group of participants and familiarity of the faces in term of accuracy ( $F(1,22)=21.57$ ;  $p=.0001$ ) and RTs ( $F(1,22)=28.26$ ;  $p<.0001$ ). Participants of the “familiar” group performed better ( $F(1,9)=20.96$ ;  $p=.0013$ ) and faster ( $F(1,9)=26.63$ ;  $p=.0006$ ) for familiar than unfamiliar faces ( $95.6\pm1.8\%$  (SE) vs.  $88.5\pm2.4\%$ , and  $646.2\pm36.1$  ms vs.  $725.7\pm44$  ms, respectively). Conversely, in the “unfamiliar” group, there were no differences between the two face sets in accuracy

( $F(1,9)=1.49$ ;  $p=.253$ ) (“familiar” faces:  $88.4\pm2.5\%$ ; “unfamiliar” faces:  $89.9\pm3\%$ ), and RTs ( $F(1,9)=1.08$ ;  $p=.325$ ) (“familiar” faces:  $593.4\pm22.8$  ms; “unfamiliar” faces:  $585.2\pm30.8$  ms). These behavioral results replicate previous studies (Bruce, 1982; Bruce et al., 1999; Hill et al., 1997; O’Toole et al., 1998; Young et al., 1986) showing that participants are better and faster at matching familiar faces across viewpoint changes as compared to unfamiliar faces.

### 2.2. Electrophysiological data

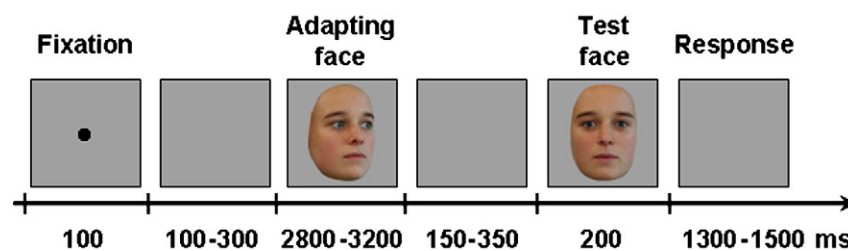
#### 2.2.1. ERPs evoked by the test faces

**2.2.1.1. P1 component.** The first clear component was the P1, who had a bilateral lateral occipital topography (Fig. 2), as in previous studies with visual stimuli, in particular with the same high-density recording system and a common average reference, see e.g. Fig. 3 in Caharel et al. (2009b). A repeated measured ANOVA with the factors electrodes (6 levels, see method), hemisphere (2), and repetition (2) was carried out on P1 amplitude, separately for the ‘familiar’ and ‘unfamiliar’ groups.

In the “unfamiliar” group, there were no significant effects at the level of the P1 (all  $p$ -values  $>.05$ ). In the “familiar” group, there was only a main effect of *Electrode* ( $F(5,45)=5.12$ ;  $\epsilon=.35$ ;  $p=.023$ ), due to larger amplitudes on PO5/6 and PO7/8 electrodes compared to the lower and more lateral channels (POO9h/10h, PO9/10, PPO9h/10h, and O1/2) (Fig. 2). All other comparisons were not significant (all  $p$ -values  $>.05$ ).

**2.2.1.2. N170 component.** The N170 peaked on slightly more anterior and lower channels than the P1, with a right hemisphere advantage, an observation also in agreement with previous studies using such visual stimuli, in particular with the same high-density recording system and a common average reference, see e.g. Fig. 3 in Caharel et al. (2009b). A repeated measured ANOVA with the factors electrodes (6 levels, see method), hemisphere (2), and repetition (2) was carried out on N170 amplitude, separately for the ‘familiar’ and ‘unfamiliar’ groups.

For the “unfamiliar” group, the amplitude of the N170 was larger in the right than in the left hemisphere ( $F(1,9)=6.52$ ;  $p=.031$ ), and on the lateral (PO9/10, P9/10, PPO9h/10h) electrodes compared to the more medial (POO9h/10h, PO7/8, P7/8) electrodes ( $F(5,45)=5.12$ ;  $\epsilon=.58$ ;  $p=.007$ ). Most importantly, a significant interaction between *Hemisphere* and *Identity repetition* ( $F(1,9)=5.38$ ;  $p=.0455$ ) was due to a larger amplitude for different than for



**Fig. 1 – Timeline of the stimulus presentation.** Following the presentation of the first (adapting) face (~3000 ms) rotated 30° in depth, a second (test) face were presented shortly (200 ms) in a frontal view of either the same or a different identity. Electrophysiological brain responses are analyzed and displayed with respect to the onset of the test face.

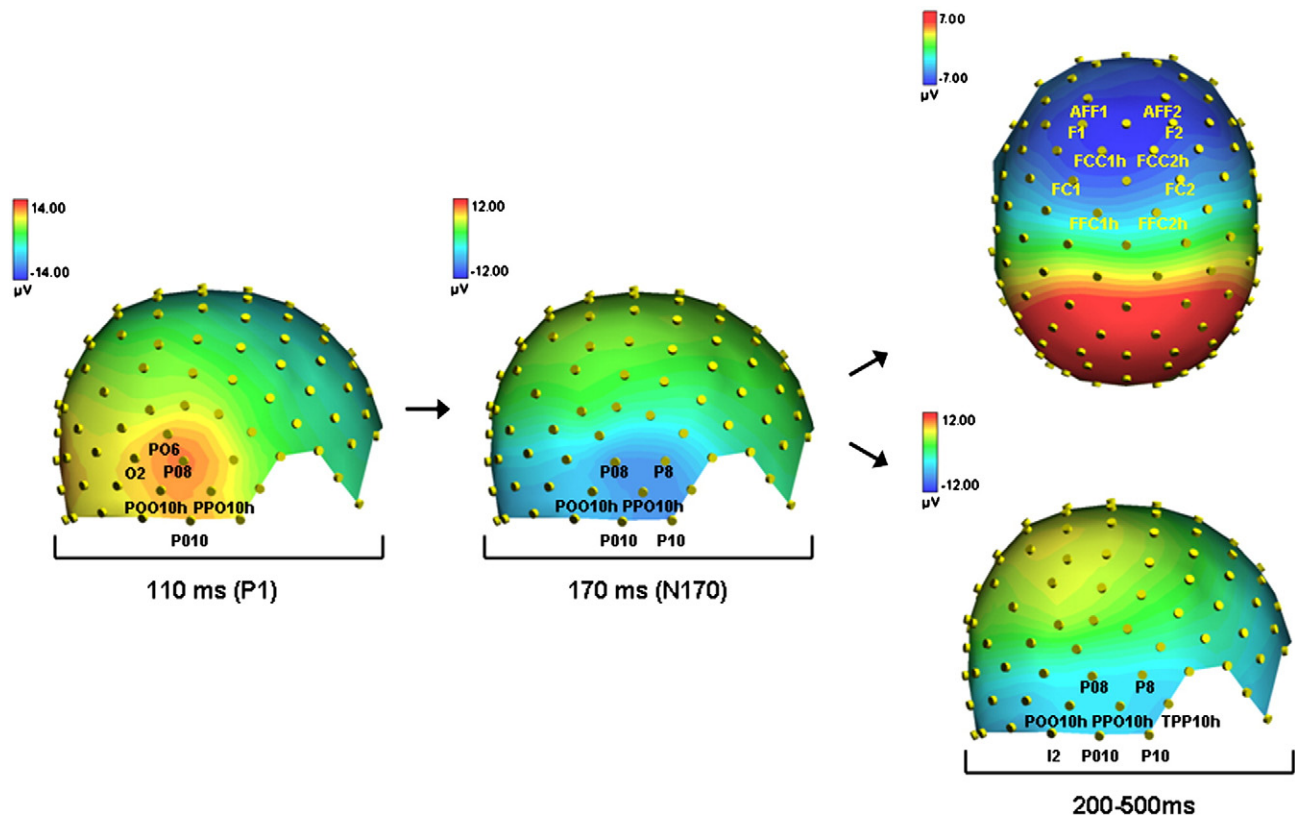


Fig. 2 – Topographical display of the sequence of evoked visual potentials of interest in the right hemisphere. The electrodes sites labeled here were used to analyze evoked potentials of interest based on their topographical map.

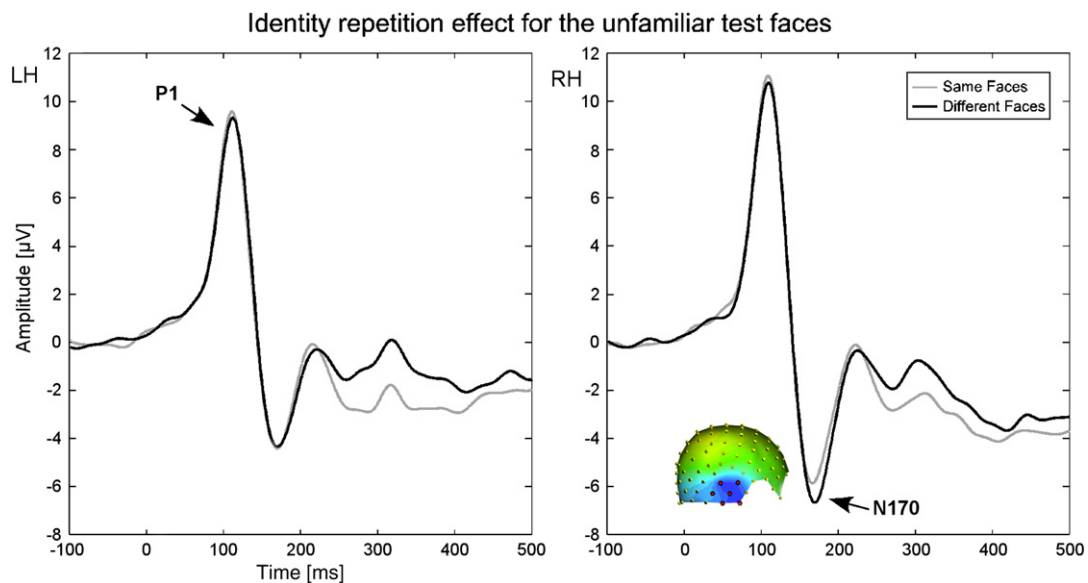


Fig. 3 – Grand average ERP waveforms for the unfamiliar test faces (always preceded by unfamiliar adapting faces) in 20 participants. For the group of participants ( $N=10$ ) who were unfamiliar with all the faces, each of the two averages include a maximum of 138 trials/participant, while only half of the face trials (69 unfamiliar face trials) were included for the other group ( $N=10$ ). The waveforms are displayed at left and right pooled occipito-temporal electrode sites (waveforms averaged for electrodes represented in a red circle on the topographical maps: P7/8, P9/10, PO7/8, PO9/10, PPO9/10h, PPO9/10h) for the different and same conditions.

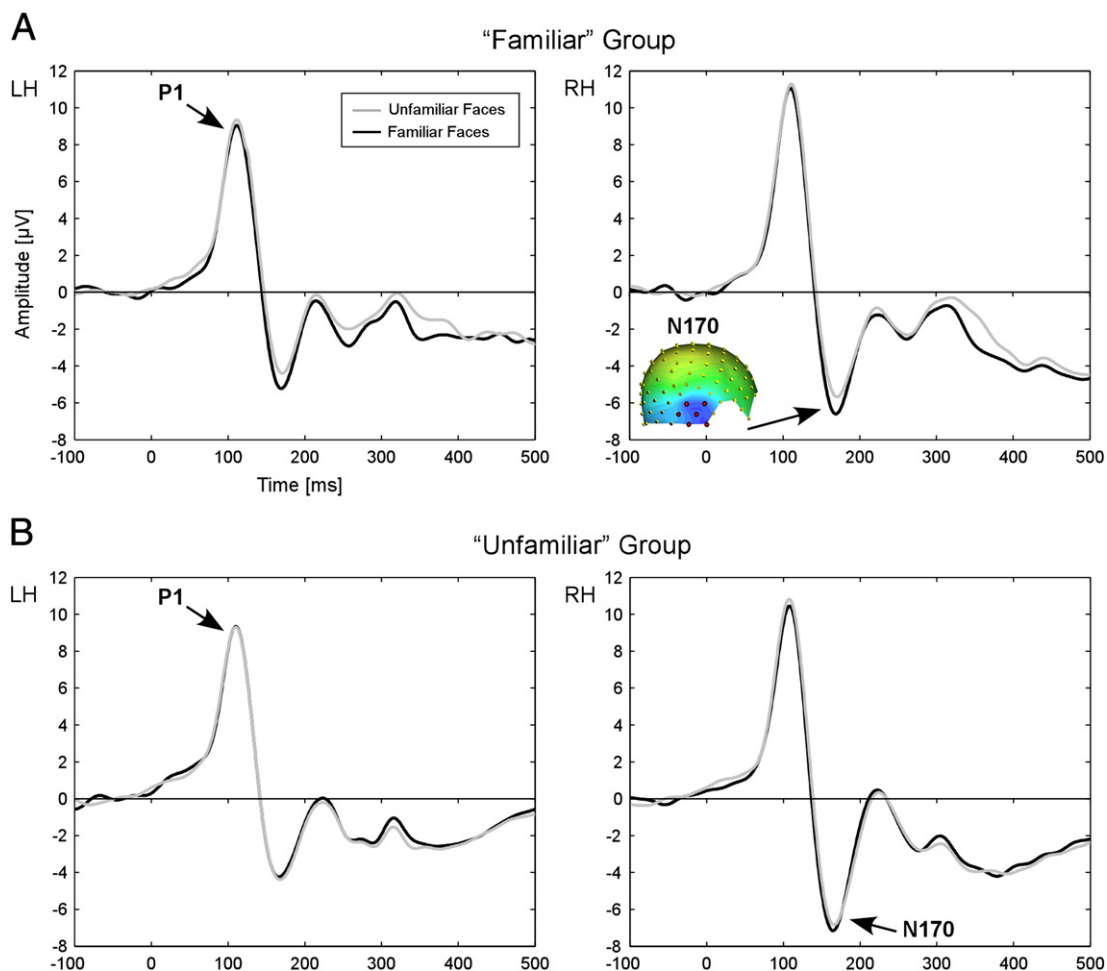


same identities in the right hemisphere ( $F(1,9)=10.64$ ;  $p=.0097$ ), but not in the left hemisphere ( $F(1,9)=.005$ ;  $p=.945$ ) (Fig. 3). As expected, there was no effect of “Familiarity” ( $F(1,9)=.22$ ;  $p=.646$ ) in this group (Fig. 4B).

For the “familiar” group, there was a significant *Hemisphere*  $\times$  *Electrode* interaction ( $F(5,45)=4.66$ ;  $\epsilon=.57$ ;  $p=.0108$ ) due to larger amplitudes on the anterior (P9/10; PPO9h/10h; P7/8) compared to the more posterior (POO9h/10h; PO7/8; PO9/10) electrodes, especially in the right hemisphere (Fig. 2). The N170 was larger for different than for same identities ( $F(1,9)=10.73$ ;  $p=.0096$ ) (Fig. 3), and for familiar than for unfamiliar faces ( $F(1,9)=8.42$ ;  $p=.0175$ ) (Fig. 4A). However, and most importantly, these effects were qualified by a triple interaction between *Familiarity*  $\times$  *Identity repetition*  $\times$  *Hemisphere* ( $F(1,9)=10.74$ ;  $p=.0096$ ). Two-factor ANOVAS for familiarity vs. identity repetition effects in each hemisphere separately revealed an adaptation effect for familiar and unfamiliar faces in different hemispheres: in the left ( $F(1,9)=11.97$ ;  $p=.0072$ ) but not in the right hemisphere ( $F(1,9)=1.93$ ;  $p=.198$ ) for familiar faces, and in the right ( $F(1,9)=11.61$ ;  $p=.0078$ ) but not in the left hemisphere ( $F(1,9)=1.06$ ;  $p=.330$ ) for unfamiliar faces (Figs. 5 and 6).

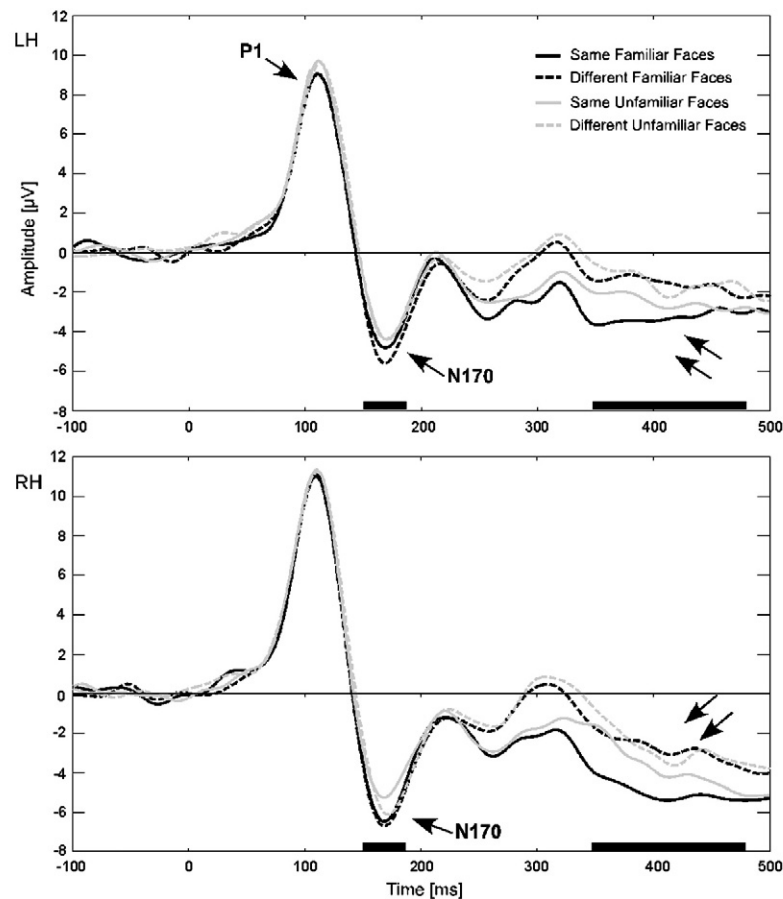
In summary, when they are repeated immediately after an adapter, unfamiliar faces (i.e., all the faces in the ‘unfamiliar’ group, half of the faces in the ‘familiar’ group) elicit a reduced N170 in the right hemisphere, but not in the left hemisphere. This observation is consistent with previous evidence (Caharel et al., 2009a). However, strikingly, when the same faces are personally familiar, the right hemisphere N170 identity adaptation effect disappears, and a significant effect appears in the left hemisphere N170.

**2.2.1.3. A 200 to 500 ms time window analysis.** For the “unfamiliar” group, a main effect of *Identity repetition* (all  $p$ -values  $<.04$ ), and a significant interaction between *Identity repetition* and *Hemisphere* (all  $p$ -values  $<.05$ ) were observed from 200 to 500 ms on fronto-central electrodes, as well as from 220 to 420 ms on posterior electrodes. The interaction reflected mainly a widespread more negative response over centro-frontal electrodes for different faces than repeated faces, which was significant in both hemispheres, but more so in the right hemisphere (RH:  $.036 < p$ -values  $<.00002$ ; LH:  $.61 < p$ -values  $<.005$ ) (Figs. 6 and 7; Table 1), with a corresponding less negative



**Fig. 4 – Grand average ERP waveforms for the “Familiar” (A) and “Unfamiliar” (B) groups by the test face at left and right pooled occipito-temporal electrode sites (waveforms averaged for electrodes represented in a red circle on the topographical maps: P7/8, P9/10, PO7/8, PO9/10, PPO9/10h, POO9/10h) for the familiar and unfamiliar faces. Note that for the “unfamiliar” group of participants, all faces were unfamiliar, and the comparison is made between the two sets of faces used in the study.**

## Event-related potential waveforms at occipito-temporal electrode sites



**Fig. 5 – Grand average ERP waveforms for the “Familiar” group at left and right pooled occipito-temporal electrode sites (waveforms averaged for electrodes P7/8, P9/10, PO7/8, PO9/10, PPO9/10h, POO9/10h) for all four conditions. Time points at which the interactions between Familiarity and Identity repetition differed significantly ( $p < .05$ ) are represented by a horizontal black line below the horizontal axis.**

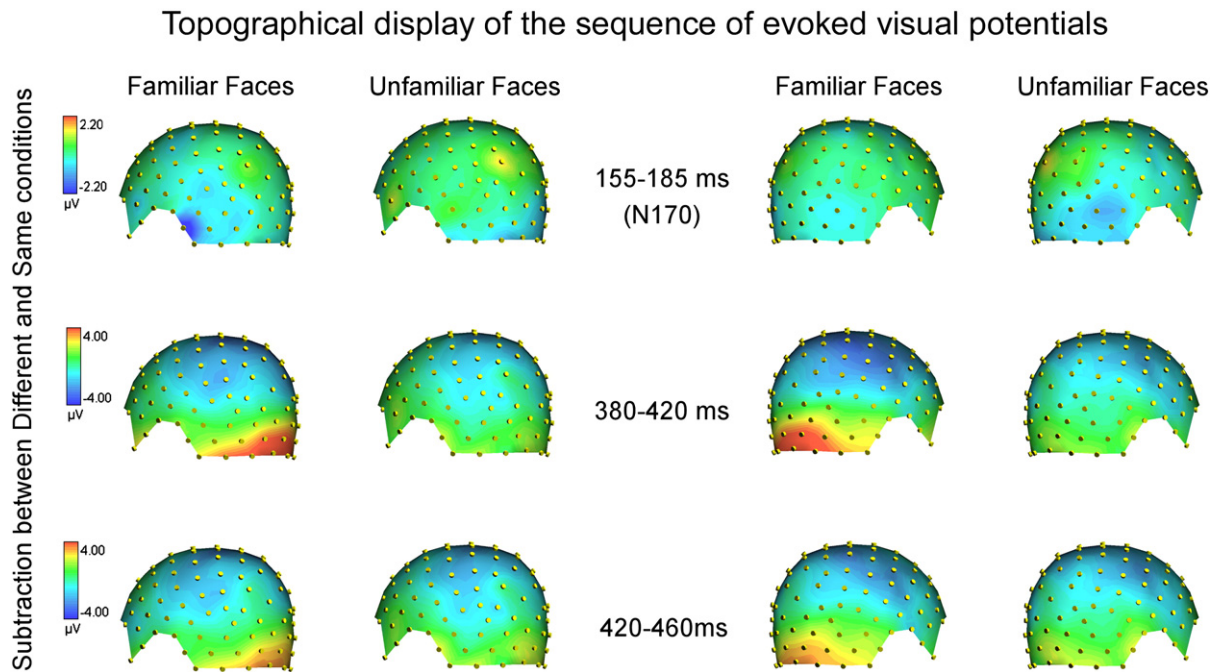
response for different faces on occipito-temporal electrodes, particularly in the left hemisphere (RH:  $.12 < p\text{-values} < .0001$ ; LH:  $.0018 < p\text{-values} < .000005$ ) in the posterior regions (Fig. 3). As expected, there was no effect or interaction involving the factor “familiarity” for this group of participants on any of the time-windows tested (all  $p\text{-values} > .05$ ; Table 1).

For the “familiar” group, there were also significant effects of *Identity repetition* (all  $p\text{-values} \leq .05$ ) from 240 to 500 ms over the fronto-central regions (Fig. 7; Tables 1 and 2) with a much larger negative amplitude for different than repeated faces on fronto-central electrodes (Tables 1 and 2; Figs. 6 and 7). At posterior sites, there was also an identity repetition effect from 280 to 500 ms (all  $p\text{-values} \leq .05$ ), with a larger negative amplitude for the same than the different condition (Table 1).

On fronto-central electrodes, an interaction between *Familiarity* and *Hemisphere* (all  $p\text{-values} \leq .05$ ) from 240 to 500 ms was due to lower negativities for unfamiliar than familiar faces, especially in the right hemisphere (Tables 1 and 2; Fig. 7). On posterior electrodes, this interaction ( $F(1,9) = 11.8$ ;  $p = .007$ ) was also found from 240 to 260 ms, showing a familiarity effect (with larger amplitude for familiar than unfamiliar faces) in the left hemisphere ( $F(1,9) = 13.4$ ;  $p = .005$ ), but not in the right hemisphere ( $F(1,9) = 1.6$ ;  $p = .69$ ) (Fig. 4A).

Most importantly, from 320 to 380 ms on fronto-central electrodes and from 360 to 480 ms on posterior electrodes, there was a significant *Familiarity*  $\times$  *Identity repetition* interaction (all  $p\text{-values} \leq .05$ ; Tables 1 and 2), with different amplitudes between same and different conditions for familiar faces ( $p < .05$ ), but not for unfamiliar faces ( $p > .05$ ; Figs. 6 and 7; Table 2).

**2.2.1.4. Complementary correlation analyses for participants familiar with half of the faces.** The N170 identity adaptation effect appearing in the left hemisphere for familiar faces appeared to correlate ( $r = -.41$ , negative amplitude difference correlated with difference in % correct) with the behavioral advantage provided by face familiarity in accuracy, but this correlation was not significant ( $p = .12$ ), due to the small number of participants. Moreover, the advantage provided by RTs appeared to correlate in an opposite direction ( $r = -.74$ , negative amplitude difference correlated with difference in correct RTs,  $p < .01$ ), so that overall this effect cannot be directly related to behavior. At later time windows, the only significant correlation with behavior (accuracy for familiar–unfamiliar faces) was found in two consecutive windows between 300 and 340 ms on fronto-central sites (identity repetition effect for familiar vs.



**Fig. 6 – Topographical maps for different time windows (between 155–185 (N170), 380–420, and 420–460 ms) represent differences between the unrepeated (different) condition compared to the repeated (same) condition for the familiar and unfamiliar faces.**

unfamiliar,  $r=.57$  and  $r=.62$ ,  $p<.05$ ; no correlation at all for correct RTs in these time windows,  $p>.3$ ). However, given the small number of participants, the significance of these correlation coefficients should be treated with caution.

#### 2.2.2. ERPs evoked by the adapting faces

In order to investigate the early familiarity effects during the presentation of the first stimulus, statistical analyses were also conducted on the ERP waveforms elicited by the first (adapting) faces of each pairs. For each group the amplitude values of the P1 and N170 components, measured within 30 ms windows for each condition, were submitted to repeated-measures analysis of variance with *Familiarity* (familiar vs. unfamiliar faces), *Hemisphere* (right vs. left), and *Electrode* as within-subject factors.

These analyses revealed that the *Familiarity* effect was significant neither on the P1 ( $F(1,9)=0.02$ ;  $p=.901$ ) nor on the N170 ( $F(1,9)=1.28$ ;  $p=.286$ ) component in the “familiar” group of participants. Additionally, the familiarity factor did not interact with any other factors (*Hemisphere*, *Electrode*; all  $ps>.43$ ). In the “unfamiliar group”, the familiarity effect was non significant on the P1 ( $F(1,9)=1.17$ ;  $p=.306$ ) and N170 ( $F(1,9)=1.76$ ;  $p=.217$ ) amplitudes, and did not interact with other factors.

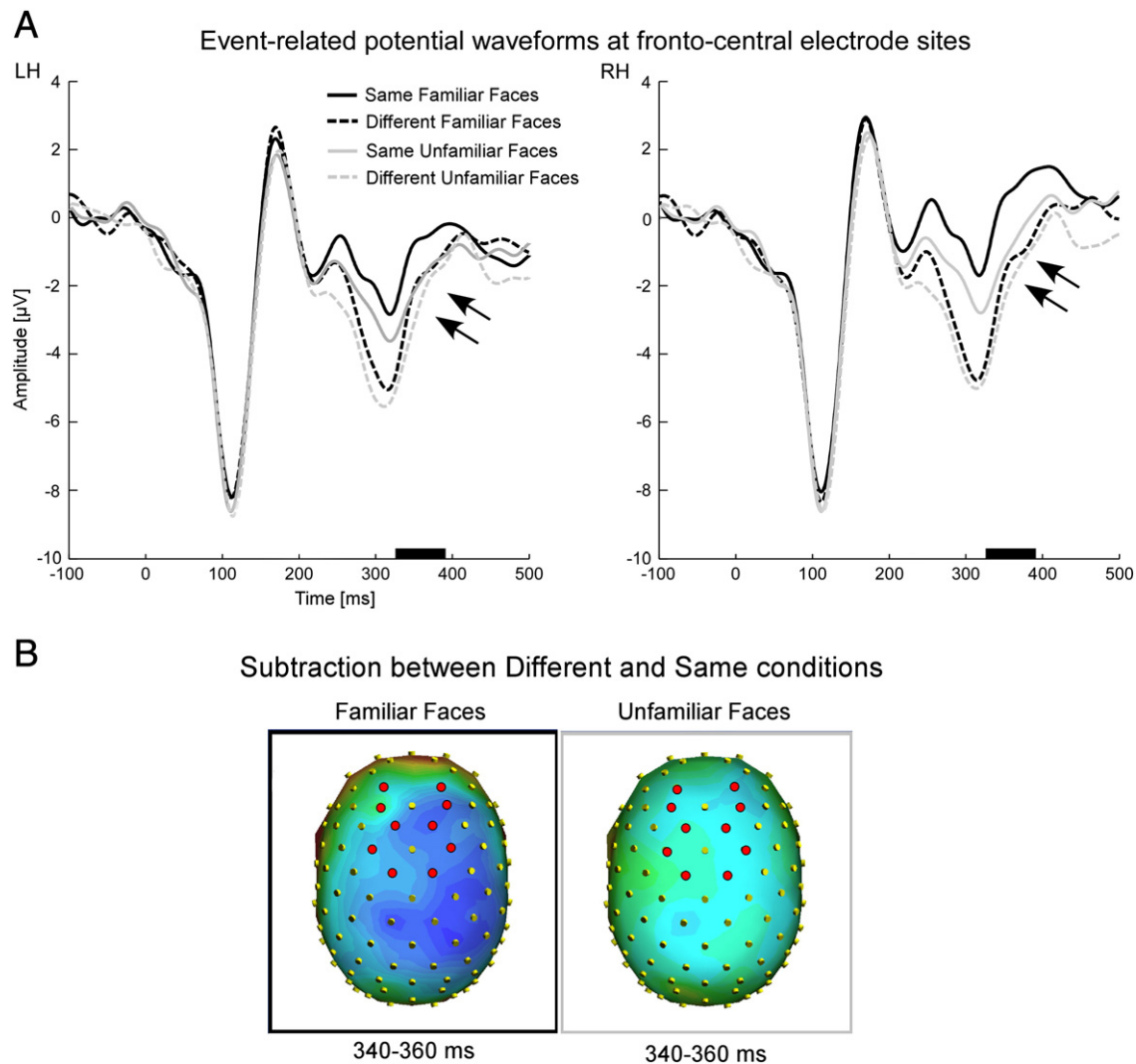
### 3. Discussion

In summary, human participants performed the face matching/discrimination task across viewpoints better with personally familiar than unfamiliar faces. The behavioral facilitation of face matching across viewpoint by familiarity—a previously reported behavioral effect (Bruce, 1982; Bruce et al., 1999; Hill et al., 1997; O’Toole et al., 1998; Young et al., 1986) was

replicated here both in accuracy rates and RTs with a set of personally familiar faces. The earliest evidence for an interaction between identity repetition and long-term familiarity of the faces was observed on the N170 component: it was smaller in amplitude when the same face identity was repeated, both for unfamiliar and familiar faces, but in the right or the left hemisphere only, respectively. At later stages of processing, effects of face identity repetition were quantitatively larger for familiar than unfamiliar faces, in line with behavioral observations.

#### 3.1. Identity adaptation of early face encoding across viewpoint changes

The N170 was reduced in amplitude after consecutive presentation of the same as compared to different facial identity. This observation is in line with previous studies (Caharel et al., 2009a; 2009b; Campanella et al., 2002; Ewbank et al., 2008; Guillaume and Tiberghien, 2001; Heisz et al., 2006; Itier and Taylor, 2002; 2004; Jacques et al., 2007; Jacques and Rossion, 2009; Kuefner et al., 2010; Martens et al., 2006). It can be taken as supporting the view that at about the time window of the N170, sufficient information has been accumulated in the human brain to individualize complex patterns such as faces (see Rossion and Jacques, 2011). Moreover, the present observation confirms recent findings that the N170 identity adaptation effect presents at least some degree of generalization across different face views (Caharel et al., 2009a). These observations are consistent with earlier studies of primate single-cell recordings indicating that despite being viewpoint-dependent, the majority of face-selective neurons in the temporal lobe show a response that decreases only gradually with increased distance from their preferred angle (Desimone et al., 1984; Perrett et al., 1985; 1991).



**Fig. 7 – (A)** Grand average ERP waveforms for the “Familiar” group at left and right pooled fronto-central electrode sites (waveforms averaged for electrodes AFF1/2, F1/2, FFC1h/2h, FC1/2, FFC1/2h) for all four conditions. Time points at which the interactions between Familiarity and Identity repetition differed significantly ( $p < .05$ ) are represented by a horizontal black line below the horizontal axis. **(B)** Topographical maps for the time window between 340 and 360 ms represent differences between the unrepeatd (different) condition compared to the repeated (same) condition for the familiar and unfamiliar faces.

The tuning response function of the N170 adaptation effect across viewpoint changes could be investigated in future ERP studies, using multiple angles of depth-rotation and angle disparity between the adapter and the target face.

### 3.2. Lateralization of early identity adaptation effects depends on face familiarity

#### 3.2.1. Reduced N170 to repeated faces in the right hemisphere: only for unfamiliar faces

Despite superior behavioral performance for matching familiar than unfamiliar faces across viewpoint, i.e. for discriminating same and different identities, the early (N170) adaptation effect in the right hemisphere, observed for unfamiliar faces, disappeared for familiar faces. That is, the N170 amplitude was of equal amplitude for repeated and different familiar faces over the right hemisphere. While, at first glance, this result is quite

surprising, we note that a recent study (Heisz and Shedden, 2009) reported a similar effect, i.e. a reduction of the N170 amplitude following unfamiliar face repetition—without changes of viewpoint—that was eliminated in the right hemisphere for faces learned with personal information. In the same vein, Henson et al. (2003) found repetition effects for unfamiliar but not for famous faces during the N170 (150–190 ms) time window. However, the present findings are particularly compelling because they were observed for personally familiar faces, across changes of viewpoint, and in parallel with behavioral data indicating that familiarity improved the matching of faces across viewpoint. Moreover, our paradigm rules out any difference between the two sets of faces as accounting for these familiarity-related modulations of the N170 adaptation effect, since there was no N170 adaptation modulation for the two sets of faces in the group of participants who were unfamiliar with these faces.



**Table 1 – Statistical analysis results within each 20 ms window from 200 to 500 ms for each group (“Familiar” and “Unfamiliar”) with factors of Familiarity (F), Identity repetition (I), and Hemisphere (H) (*p*-values are mentioned) in occipito-temporal and fronto-central electrode sites.**

Occipito-temporal regions											
“Familiar” group						“Unfamiliar” group					
	F	I	F×I	F×H	I×H		F	I	F×I	F×H	I×H
200–220 ms						200–220 ms					
220–240 ms						220–240 ms					0.0400
240–260 ms				0.0075		240–260 ms		0.0024			
260–280 ms						260–280 ms		<0.0001			0.0414
280–300 ms		0.0174				280–300 ms		0.0001			0.0005
300–320 ms		0.0032				300–320 ms		0.0012			<0.0001
320–340 ms		0.0026				320–340 ms		<0.0001			0.0007
340–360 ms	0.0354	0.0005				340–360 ms		<0.0001			0.0009
360–380 ms		0.0014	0.0394			360–380 ms		0.0001			0.0362
380–400 ms		0.0054	0.0219			380–400 ms		0.0082			
400–420 ms		0.0160	0.0374			400–420 ms		0.0358			0.0067
420–440 ms		0.0177	0.0356			420–440 ms					
440–460 ms		0.0102	0.0381			440–460 ms					
460–480 ms		0.0159	0.0113			460–480 ms					
480–500 ms		0.0461			0.0250	480–500 ms					
Fronto-central regions											
“Familiar” group						“Unfamiliar” group					
	F	I	F×I	F×H	I×H		F	I	F×I	F×H	I×H
200–220 ms						200–220 ms					0.0388
220–240 ms						220–240 ms		0.0001			0.0074
240–260 ms		0.0498		0.0176		240–260 ms		0.0043			0.0290
260–280 ms		0.0203		0.0110		260–280 ms		0.0001			0.0074
280–300 ms		0.0008		0.0049		280–300 ms		0.0001			<0.0001
300–320 ms		0.0002		0.0052		300–320 ms		0.0008			<0.0001
320–340 ms		0.0005	0.0495	0.0104		320–340 ms		0.0008			0.0015
340–360 ms		0.0016	0.0247	0.0265		340–360 ms		0.0001			0.0022
360–380 ms		0.0036	0.0348	0.0137		360–380 ms		0.0005			0.0024
380–400 ms		0.0138		0.0439		380–400 ms		0.0034			0.0022
400–420 ms		0.0675		0.0398		400–420 ms		0.0001			0.0007
420–440 ms		0.0507		0.0417		420–440 ms		0.0146			0.0005
440–460 ms		0.0341		0.0057		440–460 ms		0.0134			0.0107
460–480 ms		0.0389		0.0010		460–480 ms		0.0130			0.0312
480–500 ms		0.0385		0.0161		480–500 ms		0.0166			0.0200

How can one account for the rather unexpected disappearance of the right hemisphere N170 identity adaptation effect for familiar faces?

Heisz and Shedden (2009) suggest that semantic knowledge about familiar faces change the way these faces are processed at early perceptual stages. However, while this may possibly explain the presence of an identity repetition effect in the left hemisphere for familiar faces (see below), it is unclear why the N170 repetition effect in the right hemisphere would disappear when semantic factors are at play.

Another explanation could be related to the fact that familiar faces (Harris and Aguirre 2008), and in particular personally familiar faces (Caharel et al., 2002, 2005, 2006; Kloth et al., 2006; Wild-Wall et al., 2008), may generate larger N170 amplitudes than unfamiliar faces (as also found here). Hence, it might be that for these personally familiar faces, the N170 amplitude has reached a maximal amplitude and can no longer be further modulated by immediate repetition of same or different facial identities.

Alternatively, it may be that matching familiar and unfamiliar faces rely on different facial cues. For instance, we found recently that N170 identity repetition effects are present in the right hemisphere if 3D shape is the diagnostic information that differs between faces but not if faces differ by color and texture cues only (Caharel et al., 2009b). However, late bilateral effects are as strong for both kinds of manipulations in the adaptation paradigm (see Caharel et al., 2009b). Thus, one factor that may contribute to the disappearance of the N170 adaptation effect here could be that participants focused more on surface- (i.e., eye color, skin texture, etc.) than shape-based information when they were presented with a personally familiar face (see also Kaufmann and Schweinberger, 2008 for the suggestion that non-spatial information such as texture plays a more prominent role for familiar than unfamiliar face processing).

Note that in the kind of paradigm used here, participants knew in advance whether the second face would be familiar or unfamiliar, because the two faces presented in a pair were

**Table 2 – Average amplitudes for every time window of 20 ms, from 200 to 500 ms, for the group of participants who were familiar with half of the faces.**

Occipito-temporal regions				
	Familiar faces		Unfamiliar faces	
	Same	Different	Same	Different
200–220 ms	–1.20±.98	–1.26±.99	–.99±.83	–1.46±1.08
220–240 ms	–1.34±1.02	–1.16±.93	–1.05±.90	–.95±1.05
240–260 ms	–2.56±.95	–2.02±.88	–2.22±.87	–1.55±.93
260–280 ms	–2.68±.97	–1.80±.98	–2.24±.93	–1.37±.74
280–300 ms	–2.19±.95	–.29±.79	–1.18±.83	.52±.78
300–320 ms	–1.70±.93	–.29±.79	–1.18±.83	.52±.78
320–340 ms	–1.77±.89	–.38±.73	–.77±.78	.65±.78
340–360 ms	–3.15±.85	–1.53±.66	–1.40±.66	–.40±.63
360–380 ms	–3.42±1.05	–1.81±.76	–2.04±.73	–1.35±.66
380–400 ms	–3.66±1.09	–1.88±.76	–2.54±.77	–2.14±.66
400–420 ms	–4.00±1.17	–2.46±.92	–3.30±.79	–2.96±.68
420–440 ms	–4.03±1.06	–2.62±.89	–3.38±.84	–3.00±.77
440–460 ms	–3.97±1.04	–2.77±.89	–3.52±.87	–2.89±.69
460–480 ms	–4.15±1.01	–3.07±.91	–3.81±.91	–3.01±.79
480–500 ms	–4.28±.89	–3.49±.81	–4.15±.84	–3.39±.74
Fronto-central regions				
	Familiar faces		Unfamiliar faces	
	Same	Different	Same	Different
200–220 ms	–.44±.87	–.68±.79	–.78±.79	–.75±1.01
220–240 ms	–.47±.95	–.99±.87	–.98±.90	–1.14±1.05
240–260 ms	.36±.98	–.41±.78	–.49±.86	–1.09±.84
260–280 ms	.11±1.05	–.98±.78	–.85±.88	–1.72±.60
280–300 ms	–.57±1.12	–2.03±.91	–1.46±.93	–2.88±.58
300–320 ms	–1.22±1.09	–2.94±.89	–2.14±.83	–3.68±.72
320–340 ms	–.96±1.09	–2.60±.86	–2.06±.74	–3.15±.72
340–360 ms	.45±1.20	–1.12±.95	–.98±.74	–1.74±.71
360–380 ms	.89±1.38	–.47±1.08	–.17±.84	–.74±.76
380–400 ms	1.30±1.41	.07±1.18	.41±.99	–.08±.92
400–420 ms	1.47±1.43	.63±1.40	.90±1.11	.65±1.13
420–440 ms	1.27±1.44	.62±1.42	.69±1.18	.44±1.28
440–460 ms	.96±1.49	.65±1.37	.50±1.22	–.10±1.27
460–480 ms	.89±1.44	.77±1.31	.70±1.13	–.01±1.32
480–500 ms	.99±1.31	.71±1.16	.93±1.05	.30±1.30

inate the two faces, so that participants may have focused more on surface reflectance information for familiar faces.

If this factor plays a role in the present study, post-N170 effects of face identity repetition should be stronger for familiar (than for unfamiliar faces), because observers would be able to use cues derived from both shape and surface-based information, which contribute additively at late stages (see Caharel et al., 2009b). This is exactly what was found here, and which will be discussed in another section below.

### 3.2.2. Reduced N170 to repeated faces in the left hemisphere: only for familiar faces

A particularly interesting and novel observation of the present study is that the early (N170) identity adaptation effect across viewpoints for familiar faces transferred to the left hemisphere. That is, whereas the identity adaptation effect on the N170 was present for unfamiliar faces in the right hemisphere only, this effect appeared in the left hemisphere only for familiar faces. This observation is novel, although we note that in a previous

study using famous faces, unprimed faces appeared to show a larger (non-significant) N170 amplitude than primed faces with a different picture on left electrode sites (see Schweinberger et al., 2002b, Fig. 2 in that study). It suggests that the early processes of face individualization involve different hemispheres, as a function of long-term face familiarity. That is, there may be distinct perceptual encoding mechanisms implicated for individualization of familiar and unfamiliar faces. A difference between the right and left hemisphere for processing of unfamiliar and familiar faces has long been reported by divided visual field studies. For example, in a task that required face identification (academic versus non-academic membership categorization), Sergent (1985) reported a right visual field advantage for both speed and accuracy, indicating a left hemisphere superiority (see also Sergent et al., 1992). In contrast, during a gender categorization task of unfamiliar faces, no visual field difference was observed (Sergent, 1985) or a superiority of the left visual field (right hemisphere) (Sergent et al., 1992). According to Sergent and collaborators, these different patterns of hemisphere asymmetry depending of task demands may be related to the task-dependent visual demands, with more elaborate processing necessitated for recognition as compared to the gender categorization. Another explanation may come from the verbal processing inherent in accessing the name of an individual or in the semantic information that must be access for membership categorization.

Such inter-hemispheric distinction was also observed by neuroimaging studies which reported increased activation in several brain areas of the left hemisphere for familiar faces (Gorno-Tempini et al., 1998; Henson et al., 2000; Pourtois et al., 2005b; Sergent et al., 1992), while unfamiliar faces have been associated with larger responses activation in the right hemisphere (Dubois et al., 1999; Pourtois et al., 2005a; Rossion et al., 2001). This has been explained by the right hemisphere dominance in the perceptual aspects and the left hemisphere dominance in the semantic aspects of face processing (Rhodes, 1985; Sergent, 1985; Sergent et al., 1992). The present results suggest that the early stages of face perception would be affected by the pre-activation of representations of different nature depending on familiarity during the presentation of adapter faces. Indeed, while familiar faces could activate specific knowledge about face identity (episodic or semantic information), unfamiliar faces devoid of underlying representations stored in memory would require the generation of new representations based on perceptual information, which may explain these lateralized effects.

### 3.3. Individual face discrimination is enhanced by familiarity at late stages of processing

The early identity adaptation effects observed here seem to be of similar magnitude for familiar faces in the left hemisphere and for unfamiliar faces in the right hemisphere. This observation suggests that perceptual encoding of both unfamiliar and familiar faces show roughly the same degree of generalization across changes in viewpoint (Caharel et al., 2009a), albeit in different hemispheres.

However, at later latencies, between 320 and 380 ms over the fronto-central regions and between 360 and 480 ms over the occipito-temporal regions, the identity repetition effects for

familiar faces were larger than for unfamiliar faces. These ERP data corroborate behavioral findings showing that familiarity enhances matching performance across viewpoints (Bruce, 1982; Bruce et al., 1999; Hill et al., 1997; O'Toole et al., 1998; Young et al., 1986, and the present study) and the amount of adaptation transfer across viewpoint changes (Jiang et al., 2007), suggesting that these behavioral effects take place at a relatively late stage of processing. This time range might correspond to the time window of the N400, an ERP component correlate of face priming occurring between 300 and 500 ms in fronto-centro-parietal regions (Bentin and Deouell, 2000; Eimer, 2000; Herzmann et al., 2004; Schweinberger et al., 1995, 2002b). A N400 priming effect was observed for personally or famous faces, but not for unfamiliar faces, leading to the suggestion that this component is related to the access of semantic information about a person (Herzmann et al., 2004; Schweinberger et al., 1995, 2002b). These observations are compatible with studies using intra-cerebral recording in epileptic patients (Barbeau et al., 2008; Dietl et al., 2005) indicating a N400 in temporal structures that is modulated by face familiarity. In fMRI, Eger et al. (2005) found generalization of the repetition effect across image changes in the anterior fusiform cortex only for familiar faces, suggesting a role of this structure in the coding image-independent representations of familiar faces. Furthermore, Rotshtein et al. (2005) reported sensitivity to (categorical) changes of identity depending on subjects' self-rated familiarity within anterior regions including the anterior temporal pole bilaterally and the right hippocampus, insinuating that these regions may provide access to identity-specific semantic information. Together with these electrophysiological and neuroimaging findings, our data suggest that the more view-independent nature of familiar faces representations during this time window may be related to a link with semantic information (Bruce and Young, 1986; Burton et al., 1999).

### 3.4. Early (N170) and late modulation by face familiarity, independently of repetition

Another interesting result of the present study was that long-term familiarity modulated the N170, with larger amplitude for personally familiar than for unfamiliar faces. The current evidence with respect to the nature of the influence of face familiarity (independently of repetition) on the N170 is rather mixed: while some studies reported an N170 amplitude increase for familiar faces (famous, familiarized, or personally familiar) (Caharel et al., 2002, 2005, 2006; Harris and Aguirre, 2008; Kloth et al., 2006; Wild-Wall et al., 2008), others reported a decrease of amplitude (Marzi and Viggiano, 2007; Todd et al., 2008). Yet, other studies did not report any difference at all (Bentin and Deouell, 2000; Eimer, 2000; Rossion et al., 1999; Schweinberger et al., 2002b).

Nevertheless, the present observations are particularly interesting, for several reasons. First, we used a relatively large set of personally familiar faces, as no other study have used before. Second, an advantage of our paradigm is that this difference between familiar and unfamiliar faces cannot be attributed to the different set of pictures used: when the exact same stimuli were presented to the group of participants who were not familiar with half of the faces, there was no difference

of N170 amplitude between the two sets of face stimuli. Third, we found an increase of N170 amplitude for the target familiar faces compared to unfamiliar faces, but this familiarity effect was not present for the adapting face (see also Jemel et al., 2003). This observation suggests that the early effect of face familiarity on the N170 may depend on the observer's expectation of encountering a familiar or unfamiliar face. Indeed, during the presentation of the adapting face, observers could not predict whether a familiar or unfamiliar face would appear on a given trial. However, an adapting (un)familiar face was always followed by a target (un)familiar face.

Besides this factor of anticipation, the huge variability across these studies in terms of the N170 modulation by long-term face familiarity could be related to various methodological factors, such as the degree of face familiarity (celebrities known through media, personally familiar, or experimentally learned faces), the task used (matching, sex categorisation, familiarity discrimination, passive viewing, etc.), the stimulus set (number of faces, format (cropped or not, color or grayscale), etc.) and perhaps the method of acquisition and analyses of EEG data (density of channel array, reference, etc.). Systematic investigations examining the impact of these factors on the N170 modulations could provide a better understanding concerning the functional implication of this component and its role in the processing of face familiarity.

Concerning later latency ranges, here familiarity effects were also found at approximately 250 (N250r) and 350 ms (N400) following stimulus onset, as reported previously (Bentin and Deouell, 2000; Eimer, 2000; Herzmann et al., 2004; Paller et al., 2000; Pfütze et al., 2002; Schweinberger et al., 1995, 2002a; Tanaka et al., 2006). While the N250r has been associated to the activation of face representation in long-term memory (Herzmann et al., 2004; Pfütze et al., 2002; Schweinberger et al., 1995, 2002a; Tanaka et al., 2006), the N400 has been attributed to the semantic memory associated to familiar faces (Bentin and Deouell, 2000; Eimer, 2000; Paller et al., 2000). Altogether, our observations suggest that the long-term memory representations of familiar faces may begin to be extracted as early as 170 ms in the occipito-temporal cortex—at least when observers can anticipate the presentation of a familiar face—and become progressively more elaborate during face processing by integrating perceptual, episodic and semantic information about a specific person.

## 4. Conclusions

To conclude, the present study provides some support to the view of an early (N170) sensitivity to individual face representations which can be generalized at least partially across viewpoint changes. However, this early identity adaptation effect displayed different familiarity-dependent patterns of hemispheric asymmetry. While this effect appeared for unfamiliar faces at right hemisphere electrode sites, the effect was absent in the right hemisphere for personally familiar faces but instead appeared over the left hemisphere. Familiar faces, activating specific knowledge about face identity, would therefore depend more on visual areas localized in the left hemisphere, whereas unfamiliar faces, having no representation stored in memory, had to create new representations based on perceptual

information, and would depend more on the right hemisphere. However, the source of the behavioral advantage in matching familiar compared to unfamiliar faces across viewpoint changes seems rather related to late processes, taking place after 300 ms in fronto-central and occipito-temporal areas.

## 5. Experimental procedures

### 5.1. Participants

Twenty paid volunteers participated in this experiment. Half of them (8 females, mean age =  $17.9 \pm 0.7$  years), were recruited in the same classroom in Louvain-la-Neuve (Belgium). They were personally familiar with half of the face photographs presented during the experiment ("Familiar" Group), as they had been in the same classroom as the people whose faces were used as the familiar set for at least a year-and-a half at the time of testing (about 30 h/week for about 9 months/year). The other 10 participants (4 women, mean age =  $21.9 \pm 1.5$  years) had never seen the faces previously ("Unfamiliar" Group). All the participants were right-handed and had normal or corrected-to-normal vision.

### 5.2. Stimuli

Forty-six different face identities without glasses, facial hair or make-up, and with neutral expression were used. Twenty-three of them were faces of high school students from the classroom from which the first group of participants was recruited, and were considered as personally familiar for this group only. The remaining twenty-three faces were unfamiliar to all of the participants. Each face was presented from two different views (frontal, and  $30^\circ$  to the right). All faces' pictures were cropped to remove background, clothing and, external features (including hair) using Adobe® Photoshop® 7.0. The resulting cropped faces were equated for mean pixel luminance using the "image/adjustments/brightness" function in Photoshop. The stimuli were shown in full color and subtended approximately  $2.8 \times 3.7^\circ$  of visual angle.

### 5.3. Procedure

After electrode-cap placement, participants were seated in light- and sound-attenuated room, at viewing distance of 100 cm from a computer monitor. Stimuli were displayed using E-prime 1.1, on a light gray background. In each trial, two faces (adapting and test faces) were presented sequentially. The adapting face was oriented  $30^\circ$  to the right, and the test face was presented from a frontal view. A trial started with a fixation point displayed at the center of the screen for 200 ms. Approximately 200 ms (randomized between 100 and 300 ms) after the offset of the fixation point, the first face (adapting face) appeared for ~3000 ms (randomized between 2800 and 3200 ms). After an interval of about 250 ms (150 to 350 ms), a second face (test face) appeared for 200 ms. Offset of the second face was followed by an inter-trial interval of about 1400 ms (1300 to 1500 ms) (Fig. 1). For half of the trials, the two faces (adapting and test) were personally familiar, for the other half they were both unfamiliar. Thus, the pairs either consisted of two familiar faces or of two unfamiliar faces. In half of the

familiar and unfamiliar trials, the second face was of the same identity as the first face ( $2 \times 2$  factorial design, familiarity  $\times$  identity repetition). To further avoid any possible pixel-based adaptation effect, the second face of each trial was 5% larger than the first face. Each face appeared equally often in the "same" and "different" conditions. Whenever the pairs of faces were different, the consecutively presented faces were always of the same gender. Participants performed an individual face matching task between the adapting and test faces, and gave their response by pressing one of two keys with their right hand (keys counterbalanced across participants). They were instructed to maintain eye gaze fixation at the center of the screen during the whole trial and to respond as accurately and as fast as possible. Participants performed 69 trials per condition (23 adapting faces repeated 3 times each in both conditions). The order of conditions was randomized within each block (6 blocks of 46 trials, 276 trials in total).

### 5.4. EEG recording

EEG was recorded from 128 Ag/AgCl electrodes mounted in an electrode cap (Waveguard, ANT). Electrode positions included the standard 10–20 system locations and additional intermediate positions. Vertical and horizontal eye movements were monitored using four additional electrodes placed on the outer canthus of each eye and in the inferior and superior areas the right orbit. During EEG recording, all electrodes were referenced to the left mastoid, and electrode impedances were kept below 10 k $\Omega$ . EEG was digitalized at a 1000 Hz sampling rate and a digital anti-aliasing filter of  $0.27 \times$  sampling rate was applied at recording (at 1000 Hz sampling rate, the usable bandwidth is 0 to ~270 Hz). EEG data were analyzed using EEprobe 3.2 (ANT, Inc.). After a 30 Hz low-pass filtering of the EEG, time windows in which the standard deviation of the EEG on any electrode within a sliding 200 ms time window exceeded 35  $\mu$ V were marked as either EEG artifacts or blink artifacts. Blink artifacts were corrected by subtraction of a vertical electrooculogram (EOG) propagation factor based on EOG components derived from principal component analyses. Incorrect trials and trials containing EEG artifacts were rejected, and the number of trials was equated between conditions. Participants' averages were baseline corrected using the 100 ms pre-stimulus epoch and then re-referenced to a common average reference.

### 5.5. Statistical analyses

#### 5.5.1. Behavior

Correct response times and percentages of correct responses were submitted to a repeated-measures analysis of variances (ANOVA) with Group ("Familiar" vs. "Unfamiliar") as the between-subjects factor, and Familiarity (familiar vs. unfamiliar faces) as the within-subject factor.

#### 5.5.2. Electrophysiology

Two clear visual components elicited by the second (test) face were analyzed: the P1 (maximal at approximately 110 ms), and the N170 (maximal at approximately 170 ms). Amplitude values of these components were measured at 6 different pairs of occipito-temporal electrodes in the left and right hemisphere where they were the most prominent (for the P1: O1/2, PO5/6,



PO7/8, PO9/10, PPO9/10h, POO9/10h, and for the N170: P7/8, P9/10, PO7/8, PO9/10, PPO9/10h, POO9/10h) (Fig. 2). Amplitudes were quantified for each condition as the mean voltage measured within 30 ms windows centered on the grand average peak latencies of the components' maximum. From 200 to 500 ms after stimulus onset, the amplitude values within successive 20 ms windows were also measured at 8 pairs of occipito-temporal electrodes (P7/8, P9/10, PO7/8, PO9/10, PPO9/10h, POO9/10h, TPP9/10h, I1/2) and 5 pairs of fronto-central electrodes (AFF1/2, F1/2, FFC1h/2h, FC1/2, FFC1/2h) (Fig. 2), where differences between the 2 conditions of interest (different vs. same faces) were observed on topographical maps.

The amplitude values within each time window for each group of participants were then submitted to separate repeated-measures analysis of variance with *Familiarity* (familiar vs. unfamiliar faces), *Identity repetition* (same vs. different identities), *Hemisphere* (right vs. left), and *Electrode* (5, 6 or 8 levels) as within-subject factors. All effects with two or more degrees of freedom were adjusted for violations of sphericity according to the Greenhouse–Geisser correction. Polynomial contrasts were performed for post-hoc comparisons.

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