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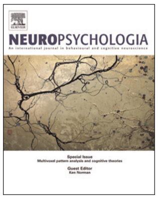

The neural speed of familiar face recognition

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ABSTRACT

Rapidly recognizing familiar people from their faces appears critical for social interactions (e.g., to differentiate friend from foe). However, the actual speed at which the human brain can distinguish familiar from unknown faces still remains debated. In particular, it is not clear whether familiarity can be extracted from rapid face individualization or if it requires additional time consuming processing. We recorded scalp EEG activity in 28 subjects performing a go/no-go, famous/non-famous, unrepeated, face recognition task. Speed constraints were used to encourage subjects to use the earliest familiarity information available. Event related potential (ERP) analyses show that both the N170 and the N250 components were modulated by familiarity. The N170 modulation was related to behaviour: subjects presenting the strongest N170 modulation were also faster but less accurate than those who only showed weak N170 modulation. A complementary Multi-Variate Pattern Analysis (MVPA) confirmed ERP results and provided some more insights into the dynamics of face recognition as the N170 differential effect appeared to be related to a first transitory phase (transitory bump of decoding power) starting at around 140 ms, which returned to baseline afterwards. This bump of activity was henceforth followed by an increase of decoding power starting around 200 ms after stimulus onset. Overall, our results suggest that rather than a simple single-process, familiarity for faces may rely on a cascade of neural processes, including a coarse and fast stage starting at 140 ms and a more refined but slower stage occurring after 200 ms.

1. Introduction

How much time do we need to recognize a familiar face? Many people would say that very little time is needed (Sagan, 2011). Part of this belief is probably related to the idea that face recognition should be fast considering how such an ability is important in daily life (i.e., to differentiate friend from foe). However, the speed of face recognition in human adults is actually rather slow and variable (Anaki and Bentin, 2009; mean or median reaction times: 400–900 ms; Anaki et al., 2007; Baird and Burton, 2008; Barragan-Jason et al., 2013, 2012; Caharel et al., 2005; Herzmann et al., 2004; Kampf et al., 2002; Ramon et al., 2011), especially compared to face detection, which is possible in 260-300 ms (Rousselet et al., 2003). The high variability of these behavioural latencies can be explained by differences in experimental procedure (e.g., go/no-go, category-verification, repetition) or the nature of stimuli used (e.g., famous faces, personally familiar faces, novel familiar faces, cropped stimuli, natural stimuli). Another source of variability is related to the fact that most studies allowed a long time for subjects to respond. Thus, subjects could use different strategies, either familiarity-based ("I know this face") or identity-based ("This is Brad Pitt, a famous actor"). Following classical hierarchical models of face recognition, familiarity-based responses are thought to be faster than identity-based responses (Bruce and Young, 1986). It is likely that subjects cannot help trying to recognize a face at the level of identity (Bruce and Young, 1986; Valentine, 2001) and hence give rather long reaction times (RTs) overall. Indeed, studies applying speed constraints reported that recognizing familiar faces from unknown faces could be achieved in 360–390 ms (minimum RTs) when repeated cropped faces were presented (Anaki and Bentin, 2009; Ramon et al., 2011). Importantly, similar minimal latencies were reported using a large set of different famous faces presented in their natural context (uncropped) without any repetition (Barragan-Jason et al., 2013, 2012), this latter finding confirming the formidable efficiency of the human visual system to process faces in natural scene.

The neural dynamics of familiar face recognition has been classically investigated using an averaging method focused on the modulation (variation in amplitude or latency) of different EEG/MEG components by familiarity. The earliest familiarity effect has

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been reported on the N170 component recorded over occipito-temporal electrodes (Caharel et al., 2007, 2005, e.g. 2002; Wild-Wall et al., 2008; faces showing higher negative amplitude than unknown ones). However, these results are inconsistent with other studies that have found an amplitude modulation in the opposite direction (e.g. Jemel et al., 2003; Todd et al., 2008) or no difference at all, especially when stimuli were not repeated or primed, or when an explicit face recognition task was used (e.g. Anaki et al., 2007; Bentin and Deouell, 2000; Caharel et al., 2014; Eimer, 2000; Eimer et al., 2012; Schweinberger et al., 2004; Zheng et al., 2012). As a result, there are two contrasted positions regarding the N170 at present. Some authors argue that it reflects mechanisms necessary for face individuation (ie. access to an individual representation of the face; Jemel et al., 2010; Rossion, 2008), while others link the N170 to holistic face representation only (e.g. Gosling and Eimer, 2011). In the first case, familiarity could occur close to the N170. In the second case, familiarity would occur in a subsequent stage.

Following the N170, the N250 component has been identified as a likely neural correlate of familiarity. This component is more negative in response to known than to unknown faces over lateral occipito-temporal electrodes as well (e.g. P8 in Leleu et al., 2010; PO8 in Pierce et al., 2011; or cluster of electrodes including P10 and TP10 in Tanaka et al., 2006). Although this component has been called the N250 component, most authors average data for their analyses over a long, and variable, period after 250 ms (230–400 ms in Gosling and Eimer, 2011; 240–300 ms in Jemel et al., 2010; and in Kaufmann et al., 2009; or 270–330 ms in Zheng et al., 2012). The N250 differs from the N250r; the latter component being elicited by the repetition of faces. However, several papers have consistently revealed an influence of face familiarity on the N250r. Specifically, Herzmann et al. (2004) found familiarity effects in a 230–270 ms segment, and Begleiter et al. (1995) found familiarity effects in the N250r peaking at 240 ms as well (for similar findings see Schweinberger et al., 1995).

In addition, some authors have focused their analysis on the onset of the differential activity between familiar and unknown faces. Begleiter et al. (1995) and more recently Zheng et al. (2012) suggest the N250 component could start around 200 ms. Similarly, Begleiter et al. (1995, Fig. 4), identified a large positive component related to familiarity, starting earlier than the usual N250, (that is, around 200 ms) and broadly distributed over anterior electrodes. More recently, Caharel et al. (2014) reported that familiarity information would start at around 200 ms after the stimulus onset. However, in their study, stimuli were repeated; it is therefore difficult to disentangle the effect of repetition from the genuine effect of familiarity. Indeed, when considering only the first presentation of their stimuli, Caharel et al. (2014) report a significant effect on the N170 component that disappears with consecutive repetitions.

All in all, several issues are still unresolved. First, the onset of the neural correlate of familiarity (with no repetition) is unknown, possibly ranging from 150 (in the N170 time-window) to 300 ms (in the N250 time-window) post stimulus onset, some studies suggesting that it should be around 200 ms. Second, as far as we know, no speed constraints (except in Caharel et al., 2014) have been applied in any electrophysiological studies on familiar face recognition allowing subjects to use different strategies. Using speed constraints would encourage participants to engage mostly in familiarity-based responses and therefore may elicit more synchronized or earlier neural familiarity effect (i.e. impacting the N170). Third, the study by Gosling and Eimer (2011) suggests that the topography of this familiarity correlate is actually not very well known since they suggest an effect on anterior electrodes rather on posterior ones where face components are usually recorded. Lastly, if some neural activity is related to familiarity, it should then also impact behaviour (e.g. RTs). Clear evidence of such relation remains to be demonstrated (see however Bentin and Deouell, 2000; Caharel et al., 2014).

Consequently, our aims in this study were to (1) identify the minimal neural latencies sufficient to explicitly recognize unrepeated familiar faces and (2) to analyze how these neural processes relate to behaviour. To address our aims, 28 subjects were asked to recognize unrepeated famous faces presented in their natural background among unknown ones using speed constraints. Our procedure was as follows. (i) We determined the onset of the differential activity between famous and unknown faces using a point by point ERP analysis of EEG recorded concurrently with the task. (ii) Additionally, as mentioned previously, there is no agreement to date on which electrodes should be included to analyze a neural correlate of familiarity and it is well known that the size of the effect varies greatly depending on which electrodes are included in ERP analyses (Rossion and Jacques, 2008). To overcome this issue, we used a complementary method called the Multi-Variate Pattern Analysis (Cauchoix et al., 2014, MVPA, 2012) that allows us to analyze and quantify the dynamics of whole-brain EEG information involved in the recognition of famous faces without any speculation about the ERP components or scalp location, this at the single trial resolution. (iii) Finally, we investigated possible relations between neural activity and behavioural reaction times.

2. Methods

2.1. Participants

Fifteen females and 13 males ($n=28$, median age: 24 yrs, range: 19–37, 25 right-handed) signed informed consent to participate in the experiment. They were mostly students in psychology or neuroscience. They were not rewarded. All subjects reported that they had normal or corrected-to-normal visual acuity. This study was performed in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and our institutional ethic review board (Comité opérationnel pour l'éthique dans les sciences de la vie/Operational Committee for Ethics in life science).

2.2. Stimuli

A set of 270 greyscale photographs of famous faces (Barragan-Jason et al., 2012) and 270 photographs of unknown faces were presented in their natural context (i.e., they were not cropped and some background could be seen). Unknown faces were chosen to be comparable in terms of quality (professional photographs). We also controlled other variables such as head orientation, paraphernalia, race and facial expressions between famous and unknown faces. Examples of photographs are presented in Fig. 1. Each image was 320 × 480 pixels and luminance and RMS contrast were comparable between famous and unknown images (luminance: $F(1538)=0.489$, $p=.61$; contrast: $F(1538)=1.005$, $p=.37$).

In order to verify that images were not different in terms of low-level features, we tried to directly decode the image category from different image features such as (1) raw grey level of pixels, which can be seen as a model of the retina, (2) Weibull parameters, which can be seen as a model of the LGN (Scholte et al., 2009) and (3) the gist; a model proposed by Torralba and Oliva (2003) that extracts orientation at different scales in the picture and performs well in categorizing natural images (this model can be interpreted as a V1-like model). We used a classification procedure identical to the one used for neural decoding (see below). None of these models allowed image category to be significantly decoded from picture features (retina-like: decoding

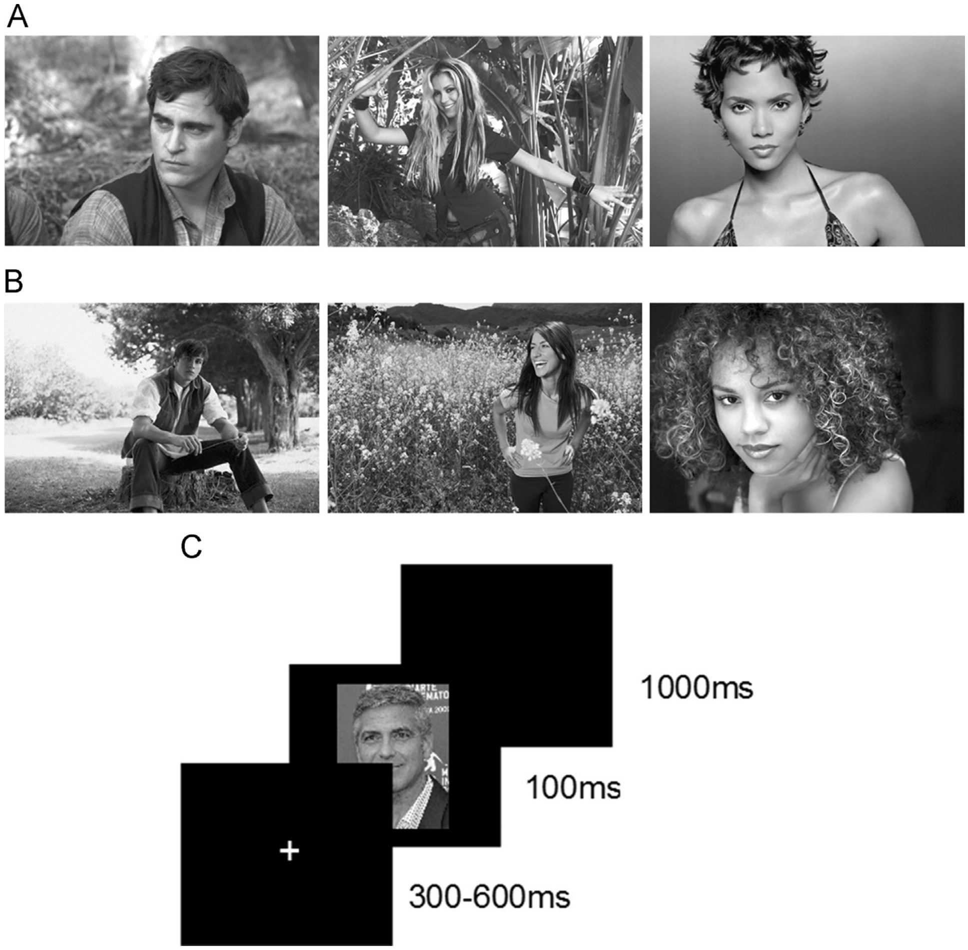

Fig. 1. Experimental design. Example of famous faces in (A) and unknown faces in (B). Example of one trial in (C). After the presentation of a fixation cross for a random interval of 300–600 ms, the stimulus was flashed on the screen for 100 ms followed by a black screen.

accuracy = 52%, $p = 0.28$; LGN-like: decoding accuracy = 52%, $p = 0.26$; V1-like: decoding accuracy = 54%, $p = 0.15$).

2.3. Experimental setting

Participants sat in a dimly-lit room approximately 90 cm away from a 19″ CRT computer screen (resolution: 1024 × 768; vertical refresh rate: 100 Hz) controlled by a PC computer. Photographs were displayed on a black background and subtended a visual angle of $\sim 7° \times 11°$ using the E-prime® software. Responses were provided through a custom-made infrared response pad.

2.4. Experimental design

The go/no-go task was divided into three blocks of 180 photographs (90 targets and 90 distractors each). Participants had to raise their fingers from the response pad as quickly as possible when a famous face (go-response) was presented among unknown faces (no-go response). Each trial started with the presentation of a fixation cross for a random interval to prevent anticipatory responses (300–600 ms). The fixation cross was followed by a photograph flashed for 100 ms and a black screen for 1000 ms. Stimuli were randomly displayed across blocks for each subject and each photograph was seen only once by each subject.

At the end of the experiment, each famous face was randomly displayed and subjects had to rate their semantic knowledge about the famous person using a scale from 0 (unfamiliar face, no information) to 6 (extremely familiar, a lot of information). Mean rate value was 2.8 across images (min:0.3 max:5.2; SD = 1.0) and 3.35 across subjects (min:0.8 max:5.1; SD = 1.0). Famous faces rated as unknown (0 on the knowledge scale) were discarded from both behavioural and EEG analyses, as were reaction times below 200 ms or above 1000 ms (Barragan-Jason et al., 2012).

2.5. Speed constraints

We developed various strategies to encourage subjects to answer as fast as they could. Stimuli were flashed quickly (100 ms) and subjects had to answer before the 1000 ms post-stimulus ended. Participants were familiarized with the experiment using a small set of stimuli (30 targets, 30 distractors) not used for the actual experiment and could repeat the training session if they wanted. After each block, including the training session, mean reaction times and false-alarm rates were displayed so that subjects could monitor their performance. Crucially, they received strong encouragement before and between blocks to answer as fast as possible. In particular, after each block, they were asked to "beat" their RT score.

2.6. Behavioural performance analyses

In order to evaluate subjects' performance, d prime (d') (discrimination performance) for each participant was computed (Rousselet et al., 2003). To obtain an estimation of the minimal processing time required to recognize targets, the latency at which correct go-responses started to significantly outnumber incorrect go-responses was determined for each subject (e.g. Rousselet et al., 2003). We applied an exact Fisher test with 30 ms time bins on RTs for each individual participant (Barragan-Jason et al., 2013, 2012; Besson et al., 2012). To correct for multiple comparisons, significance had to last 60 ms at least and the beginning of the first significant bin was considered as the minimum RT (Barragan-Jason et al., 2013, 2012; Besson et al., 2012). A minimal reaction time can’t be computed if the distribution of hits does not reach a certain threshold above the distribution of false alarms. Thus, it was not possible to compute a minimal reaction time for all participants.

We also calculated minimal RTs across all trials using 10 ms time bins. Across-trials analyses have been used in previous studies (Barragan-Jason et al., 2013, 2012; Besson et al., 2012; Rousselet et al., 2003) and are like building a “meta-participant”, reflecting the performance over all the population. The beginning of the first significant time bin (χ^2-test, $p < 0.05$), followed by at least five significant consecutive bins was considered as the minimal RT (Besson et al., 2012).

2.7. EEG recording

We recorded neural activity from 32 electrodes mounted in an elastic cap with the addition of extra occipital electrodes in accordance with the 10-20 system (Oxford Instruments), using a SynAmps amplifier system (Neuroscan). The ground electrode was placed along the midline, ahead of Fz, and impedances were systematically kept below 5 kΩ. Signals were digitized at a sampling rate of 1000 Hz and low-pass filtered at 100 Hz. Potentials were referenced on-line to the Cz electrode and averaged-referenced off-line. EEG data analysis was performed using EEGLAB (Delorme and Makeig, 2004), an open source toolbox running under Matlab (Mathworks).

First, EEG data were down-sampled to 256 Hz and then digitally filtered using a bidirectional linear filter (EEGLab FIR filter) that preserves the phase information (pass-band 0.1–40 Hz). For two of the participants, one of the channels also had to be excluded from analysis because of the presence of significant permanent artifacts. Continuous data were then manually pruned from non-stereotypical artifacts such as high amplitude and high-frequency noise (muscle) as well as electrical artifacts. All remaining data were then submitted to Infomax Independent Component Analysis (Infomax ICA) using the runica algorithm (Makeig et al., 1997), from the EEGLAB toolbox. For each subject, we visually identified and rejected one to three well-characterized Independent Components (ICs) for eye blink and lateral eye movements (Delorme et al., 2007). Scalp maps, power spectrum and raw activity of each component were visually inspected to select and reject ICs which were artifacts.

A total of 540 epochs for each individual participant were extracted (−50 to 700 ms) and baseline-corrected (−50 to 0 ms). Only trials with correct responses (correct go-responses of famous faces and correct rejection of non famous faces) were considered for EEG analyses (mean percentage of incorrect rejected epochs across participants: 30.4%; SD=7; range: 15–40). Epochs containing artifacts were excluded from further analysis (mean rejected epochs across subjects: 12%, SD=5; range: 2–23). Following this entire procedure, the number of epochs in the correct famous face condition (mean across subjects=120) was outnumbered by the number of epochs in the correct non-famous condition (mean across subjects=188). To get rid of the difference in the signal-to-noise ratio between both conditions, we subsampled randomly for each subject the largest condition to keep an equal number of epochs in each condition. We did this before the ERP analyses and for each cross validation of the MVPA analysis.

2.8. ERP analyses

We performed classical peak analysis for P100 and N170 components: amplitudes were quantified for each condition as the mean voltage measured within 30 ms windows centered on the grand average peak latencies of the component's maximum amplitude (Cauchoix et al., 2014; Rossion and Caharel, 2011; Rossion and Jacques, 2008). The P100 component analysis is important to investigate a potential effect of low-level visual information on the differential activity between targets and distractors (Rossion and Caharel, 2011**;** Cauchoix et al., 2014). For the N250 component, mean amplitude was calculated within three different time-windows of interest (N250a: 200–250 ms; N250b: 250–300 ms; N250c: 300–350 ms) based on visual inspection and previous studies (Gosling and Eimer, 2011; Pierce et al., 2011; Wu et al., 2012; Zheng et al., 2012) rather than the peak latency approach used for the N170, because N250 peaks are difficult to reliably measure in individual subjects. N250c is sometimes called the face-N400a in the literature (Kamijo and Takeda, 2014; Webb et al., 2010). To estimate reliable differences in peak amplitude while limiting possible confounding issues due to multiple comparisons, we ran a paired two-tailed permutation test based on the *t*max statistic (Blair and Karniski, 1993) using a family-wise alpha level of 0.05 (32 comparisons) for each component (P100 and N170) (Cauchoix et al., 2014). The permutation test guarantees protection against multiple comparisons (Maris and Oostenveld, 2007). All statistic analyses were performed using the Mass Univariate ERP toolbox (Groppe et al., 2011) written in MATLAB.

In order to precisely track down the time course of familiarity-related information, the same statistical analysis was used for comparing ERPs evoked by familiar faces vs. unknown faces. For this analysis, we considered all time points between −50 and 700 ms (192 time points) across all 32 electrodes (i.e., 6144 comparisons) (Cauchoix et al., 2014).

Because the use of speed constraints (i.e., using a go no-go task as in the present study) may lead to a difficulty to clearly disentangle late effects of familiarity from motor effects (i.e. after 250–300 ms), we performed a complementary analysis using data we have already published (Cauchoix et al., 2014). Indeed, the subjects who performed the current study also performed a control task where they had to categorize unknown faces among animal faces, a task which is however performed faster than the current one reported in this study. This comparison is thus conservative. We can thus track the time course of motor information and look at the possible motor effect on the different time windows of interests (go-responses to unknown faces from the previous task compared to no-go responses to unknown faces from the current task)**.**

2.9. Multivariate Pattern Analysis (MVPA)

MVPA was conducted following a previous published methodology (Cauchoix et al., 2014) on single-trial ERPs: A linear classifier was trained to decode the presence of a target vs. distractor in single trials from individual time bins of the EEG signal across all electrodes. We derived an accuracy measure by averaging the performance of the classifier over multiple random splits of the data (see Fig. 2 below). Such decoding analysis characterizes the temporal evolution of the category signal across the whole brain. Each input feature (electrode potential) was normalized (*Z*-score) across trials and a linear Support Vector Machine (SVM) was used as classifier (libsvm implementation by Fan et al., 2005). The classification procedure was as follows: (1) the trial set was equally split into a training set and a test set, each containing an equal proportion of famous and unknown images; (2) an optimal cost parameter C was determined through line search

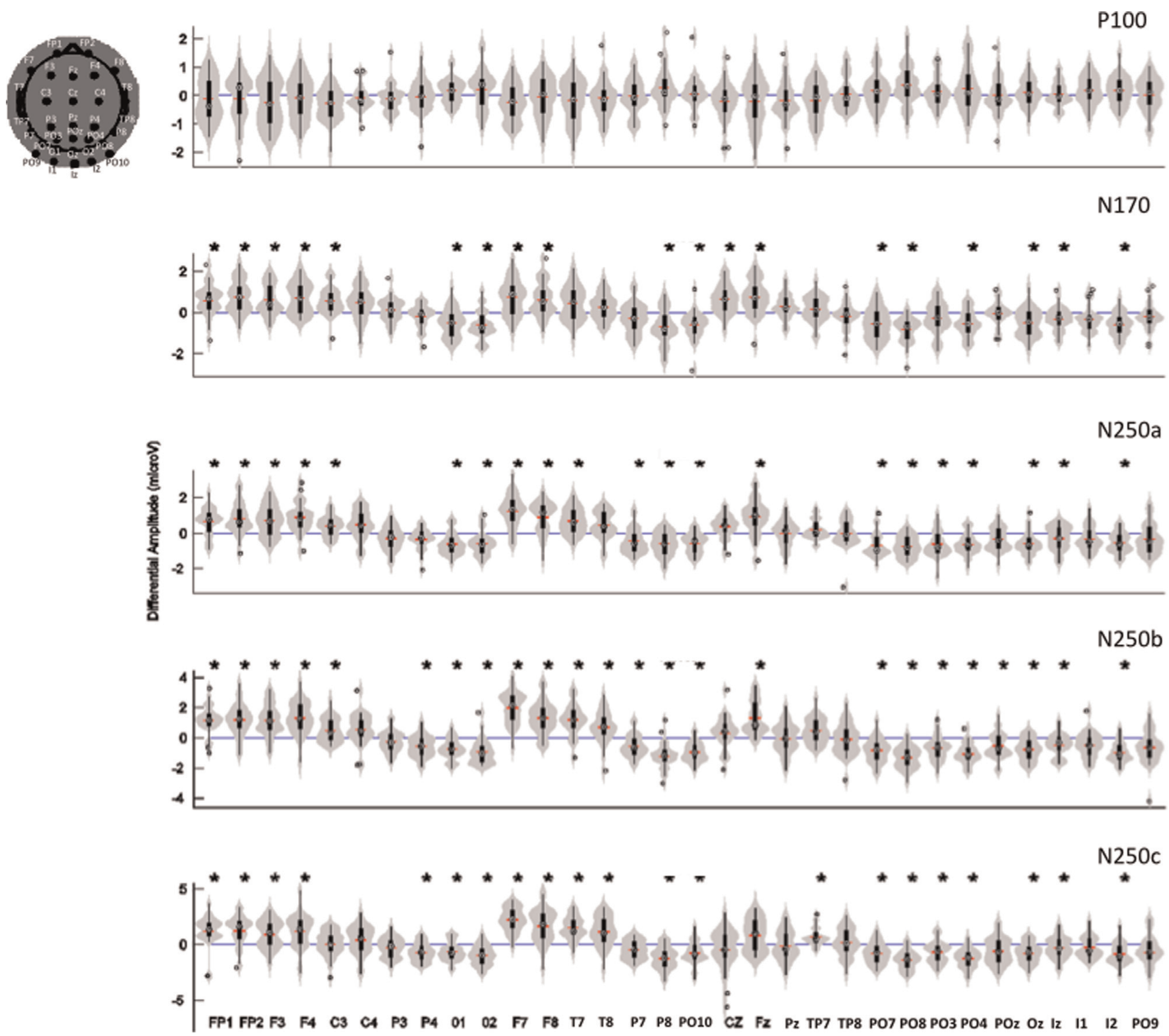

Fig. 2. Peak analysis of the different EEG components (from top to bottom: P100, N170, N250a, N250b, N250c) following new recommendations about how to present data (Allen et al., 2012). Violin plots and boxplots represent the paired differences between famous and unknown face neural responses. Significance is indicated by * ($p < 0.05$ after correction for multiple comparisons).

optimization using 8-fold cross-validation on the training set of images; (3) an SVM classifier was trained and tested on each set. For each subject, this procedure was repeated over 100 times where different training and test sets were selected each time at random. A single measure of accuracy was obtained by averaging the classification performance over all repetitions. A measure of chance level was obtained by performing the same analysis on permuted labels. This allowed us to estimate the latency of task-related information across all participants via a paired, two-tailed permutation test (accuracy measured on permuted vs. non-permuted labels; $p < 0.01$) based on the *t*max statistic (Blair and Karniski, 1993) using a family-wise alpha level of 0.05 (i.e., 192 comparisons). Reported decoding latencies correspond to the earliest significant bin (Cauchoix et al., 2014).

3. Results

3.1. Behavioural performance

To obtain an estimation of the minimal processing time to recognize a familiar face, we first calculated minimal reaction time for each subject. Subjects performed the task as soon as 546 ms (minimum RT averaged across participants, SD=79; range: 390–720 ms; minimum RTs could not be calculated for 6 subjects). Minimum RTs over all trials was 460 ms. Mean median RT was 625 ms (SD=76; range: 473–779 ms). Mean d' was 1.32 (SD=0.44, range: 0.46–2.12). All subjects performed above chance (binomial test; $p < .001$).

3.2. ERP analysis

P1, N170 and N250 ERP components could be readily identified on electrodes P8, PO8 and PO10 where the N170 component is usually maximal (Rossion and Caharel, 2011; Rossion and Jacques, 2008). Peak analysis revealed that P1 component (maximal on PO4 and PO8: 5.9 μV at 109 ms and 5.8 μV at 117 ms respectively) did not present a familiarity effect on any electrode (Fig. 2).

ERP peak analyses revealed a significant N170 modulation by familiarity on several electrodes (19 electrodes; Fig. 2). The greatest (more negative) amplitude to famous faces relative to unknown ones was reported on P8 ($t(27) = -4.93$; $p < 0.001$)

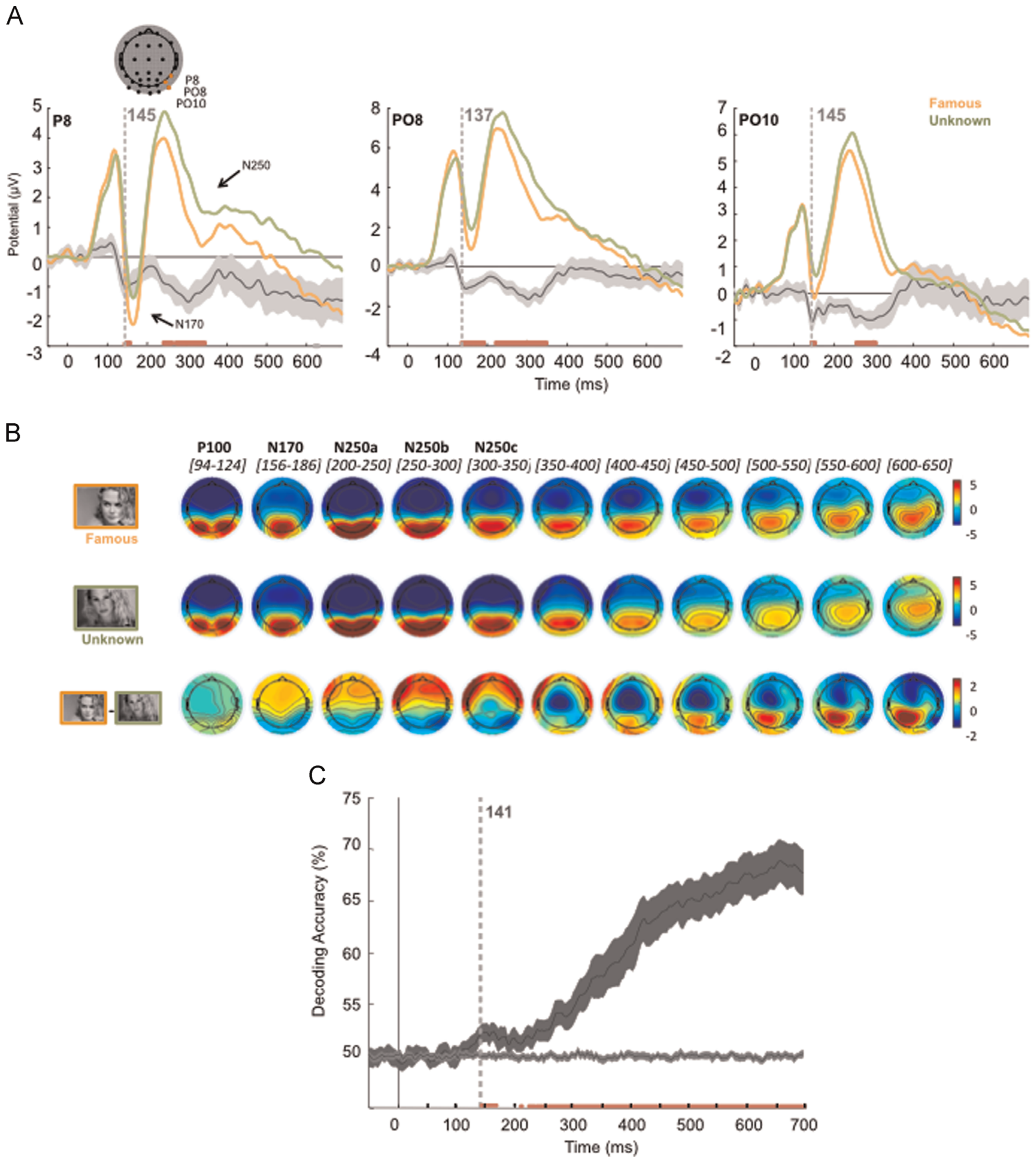

Fig. 3. Results from all participants ($n=28$). (A) Grand average waveforms on occipito-temporal electrodes P8/PO8/PO10 for famous face targets in orange and unknown face distractors in green. Positions of the electrodes are indicated in orange on the scalp topography (top left). Grey curves indicate the differential activity between the two conditions with confidence interval in light grey. Red rectangles plotted on the *x* axis indicate time bins when the two conditions differ significantly (see method for details). Vertical dot lines indicate the first significant time bin where target stimuli differ from non target stimuli revealing the onset of the differential activity. (B) Topographical maps from grand-averaged data of all participants representing the scalp distribution for each condition (Famous faces, top), Unknown faces, (middle), and the subtraction between the two conditions (bottom) during time-windows specified on the top (from 94 to 650 ms). (C) 95% confidence interval decoding accuracy across subjects on true and randomized labels. The earliest significant decoding onset is indicated by the vertical dotted line. Red rectangles plotted on the *x* axis indicate time bins when the real decoding is significantly different from chance.

(Fig. 3A). Time point ERP analyses revealed significant differences between famous and unknown faces as soon as about 140 ms on most electrodes (Fig. 3A). This latency is consistent with the onset of the N170 time-window.

Similarly, a familiarity effect was reported after 200 ms, during the N250, for each time-period investigated (N250a: 200–250, N250b: 250–300 and N250c: 300–350). This effect was observed in most electrodes (21, 24 and 21 for the N250a, N250b and the N250c respectively; Fig. 2). Additionally, time point ERP analyses revealed significant differences occurring after 200 ms during the N250 time-windows (Fig. 3A). Overall, familiarity effects could be observed broadly on posterior but also anterior electrodes (Figs. 2

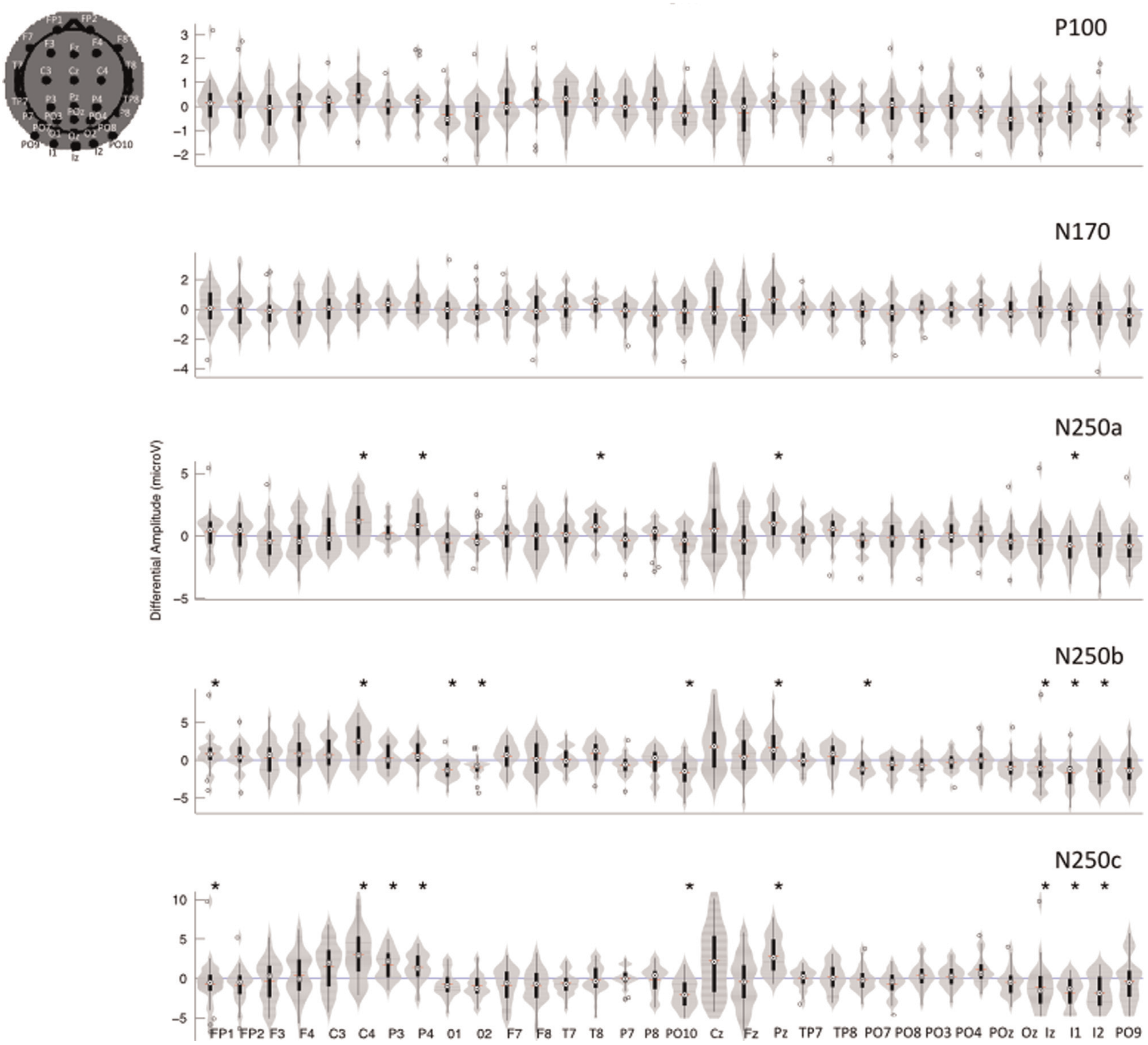

Fig. 4. Peak analysis of the different EEG components (from top to bottom: P100, N170, N250a, N250b, N250c) following the new recommendations (Allen et al., 2012; Hupé, 2015). Violin and boxplots represent the paired differences between neural responses from go responses for unknown faces and no go responses for unknown faces. Significance is indicated by * ($p < 0.05$ after correction for multiple comparisons).

and 3B).

Finally, we look at the time course of motor effect on the ERP components. We compare the differential activity (Fig. 4) between go-responses for unknown faces (from a previous study, see Section 2) and no-go responses for unknown faces (current study). No effect was found on the two earliest time windows (ie., P100 and N170). However, results indicated a significant motor effect on the N250a and the N250b time windows (Fig. 4).

3.3. MVPA analysis

Because we report a widely distributed familiarity effect over most electrodes, we performed a complementary whole brain MVPA analysis on EEG signals that allows us to analyze all information available across all electrodes (Cauchoix et al., 2014, 2012). This procedure has the advantage to quantify the magnitude of and to summarize the neural information available for the task without any loss of specificity. It also permits us to visualize the global dynamics of the information related to familiarity at the single-trial level.

The neural dynamics of face recognition was thus estimated using a single trial temporal decoding accuracy measure for each subject averaged across participants (Fig. 3C). A first significant bump of activity is reported between 140 and 180 ms (Fig. 3C). This transitory activity was followed by a decrease of decoding power that went down to chance level. Then, a second significant increase of activity started at about 200 ms after stimulus onset and continued to increase until it reached 70% of accuracy at 600 ms. The latency of the first transitory decoding activity fits with the N170 time-window, whereas the increase of activity after 200 ms fits with the onset of the N250 time-window.

3.4. EEG and behaviour

We then investigated whether the early EEG modulation by familiarity could be related to behaviour. To do so, we defined two groups of subjects: Group 1 was composed of the half of participants showing the biggest differential activity on P8 during the N170 time-window, whereas Group 2 was composed of the other half of the subjects (Fig. 5A). As a result, Group 1 presented a

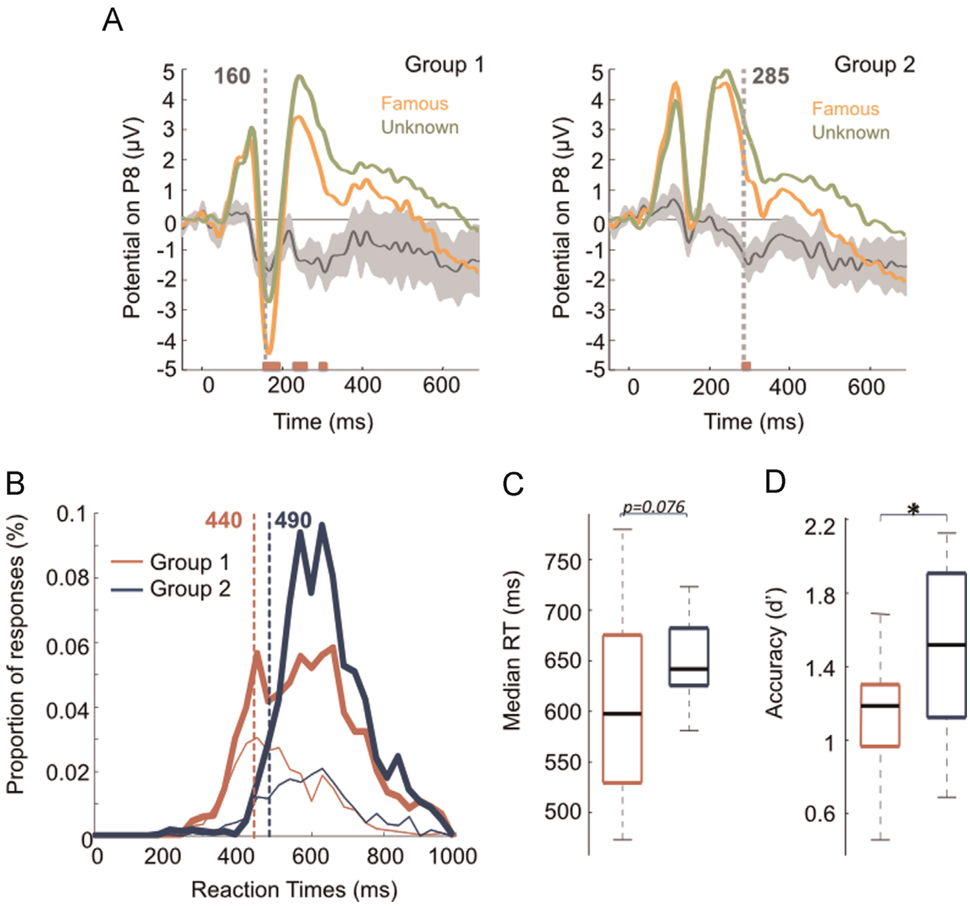

Fig. 5. EEG and behavioural results contrasting Group 1 (subjects presenting the biggest familiarity effect on the N170 on P8 (half of the subjects, $n=14$)) from Group 2 (the other half, $n=14$). (A) Analysis presenting grand average waveforms for the two groups separately (Group 1 on the left, Group 2 on the right) with famous faces in orange and unknown ones in green. Vertical dot lines indicate the first significant time bin when target differ from non target stimuli revealing the onset of the differential activity. Red rectangles, on the *x* axis, represent the period of time when the two conditions differ significantly. (B) Across-trial distribution of RTs for the two groups showing a shift in the distribution of Group 1 towards the left. Note the first peak of hits, accompanied by a peak of false alarms, present for Group 1 and not for Group 2. Vertical dot lines indicate minimum RTs across trials for each group. Thick lines: hits. Thin lines: false-alarms. (C) Median RT for both groups showing a tendency for Group 1 to be faster than Group 2. (D) Accuracy (d') boxplots from Group 1 and Group 2 showing a significant difference between the two groups ($p<.05$) in favour of Group 2.

modulation by familiarity as fast as 160 ms during the N170 time-window. On the contrary, Group 2 showed a familiarity effect at about 280 ms after stimulus presentation. Interestingly, across-trial comparison between RT distribution of the two groups (Fig. 5B) revealed that Group 1 was faster (minimum RT across trials: 440 ms) than Group 2 (minimum RT across trials: 490 ms). Importantly, distributions of RTs were different: Group 1 distribution showed an early first “peak”, accompanied by a large peak of false alarms, followed by a second peak. In contrast, distribution of RTs of Group 2 was shifted to the right and its distribution matched with the second peak of Group 1. Across-subject analysis of median reaction times showed a tendency for Group 1 to be faster than Group 2 ($t(27)=-1.85$; $p=0.076$; Fig. 5C). Minimum reaction times could not be calculated for 3 of the 14 subjects of Group 1 and for 3 of the 14 subjects of Group 2 and were thus not analyzed. Additionally, participants in Group 1 were less accurate (d') than participants of Group 2 ($t(27)=-2.23$; $p=0.034$; Fig. 5D). We verified that Group 1 and Group 2 did not present any difference in their knowledge about the famous faces. A paired *t*-test between the rated familiarity scores for the famous faces revealed that Group 1 (mean: 2.72, SD=1.2) and Group 2 (mean: 2.63, SD=1.1) did not differ in their semantic knowledge about celebrities ($t(26)=-0.213$; $p=0.89$).

Finally, we performed a trial analysis in order to assess whether the EEG modulation occurring during the N170 time window could vary by trial. We performed a single trial temporal decoding for fast trials (< median RT) and slow trials (> median RT) separately (Fig. 6). The decoding analysis revealed that the fastest trials were decoded faster (i.e., onset at 145 ms, during the N170 time window) than the slowest trials (onset at 270 ms, during the N250b time window).

4. Discussion

Our findings revealed an effect of familiarity at several latencies including the N170 and the N250 time-windows. Both ERP and MVPA analyses revealed a significant effect of familiarity for unrepeated famous faces as fast as 140 ms (in our task, subjects were required to recognize the faces as fast as they could). Importantly, this early familiarity for faces was related to behaviour (i.e., participants' strategies). Our results strongly suggest that neural processing taking place as fast as 140 ms are involved in early familiarity for unrepeated familiar faces but also suggest that rather than a simple single-process, familiarity for faces is a more complex phenomenon that may imply a cascade of processes, including a coarse and fast stage starting at 140 ms and a more refined, slower, stage occurring after 200 ms.

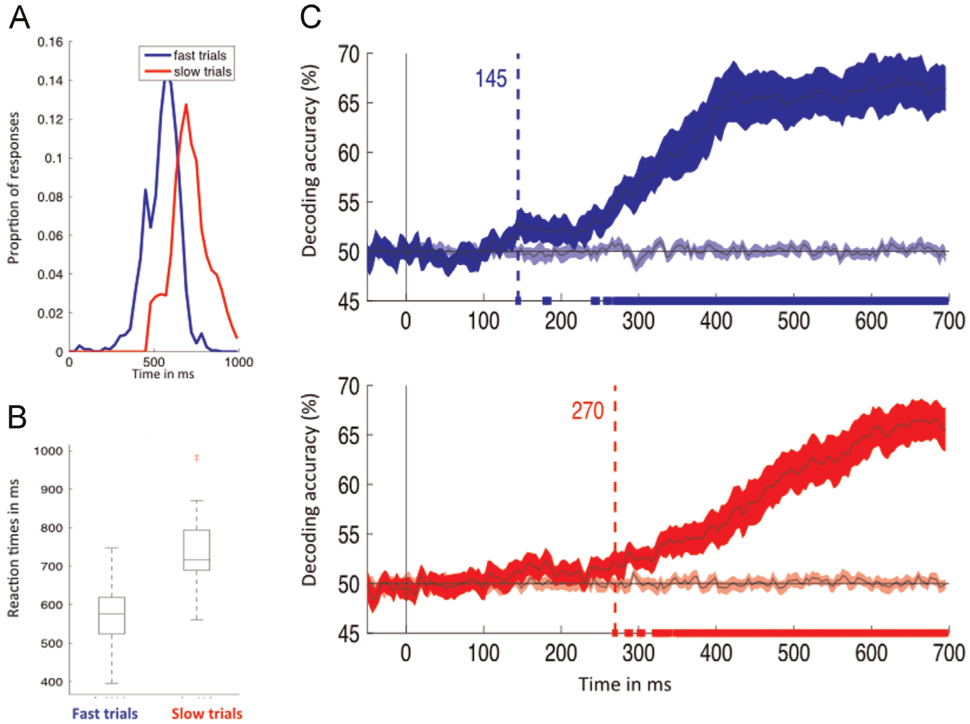

Fig. 6. Results from a trial analysis comparing fast (< median RT in blue) and slow trials (> median RT in red). (A) RT distribution for fast and slow RTs across all subjects. (B) Bloxplots for fast and slow RTs across all subjects. (C) 95% confidence interval decoding accuracy across trials on true and randomized labels. The earliest significant decoding onset is indicated by the vertical dotted line. Rectangles plotted on the *x* axis indicate time bins when the real decoding is significantly different from chance.

4.1. *Fast neural processing of familiarity*

The aim of the current study was to track down the minimum neural latency underlying face recognition. Using both ERP analyses and MVPA on EEG signal recorded during a go/no-go task run under speed constraints and with no repetition of faces, we identify for the first time a minimal differential activity related to familiarity for faces starting as soon as 140 ms after stimulus presentation (Fig. 3) and we show that the N170 component is modulated by familiarity. This first result confirms previous studies showing an increase of the N170 amplitude between familiar and unfamiliar faces (Caharel et al., 2007, 2005, 2002; Wild-Wall et al., 2008). However, most studies did not report such an effect and rather suggest that the N170 component indexes face individuation (Caharel et al., 2014; George et al., 2005; Itier and Taylor, 2004; Rossion and Caharel, 2011) whatever the stimulus state (familiar or unfamiliar face; Rossion, 2008). Our results suggest that some form of familiarity could occur concomitantly with the N170 and thus concomitantly to face individuation.

Subjects with a large modulation of the N170 performed the task quicker (smaller overall minimal RT and tendency for fastest across subjects median RTs) than subjects with a small modulation of the N170. This timing advantage is accounted for by the presence of a bimodal distribution of RTs for subjects presenting a large N170 modulation. As hypothesized in the introduction, modulation of the N170 in the present study could be related to the use of speed constraints, which may have encouraged subjects to use faster strategies and which may also have enhanced neuronal synchronization. However, we report a faster effect than reported in a previous study where similar speed constraints were applied (Caharel et al., 2014) (210 ms in Caharel et al. (2014) vs 140 ms in our study). Indeed, Caharel et al. (2014) report a N170 modulation during the first presentation of familiar faces compared to unknown ones but this effect disappeared after repetition. A possibility is that the current study used single presentation of a large number of natural stimuli (270 different identities vs 26 different including subjects' own faces repeated 8 times in Caharel et al. (2014)). This allowed us (1) to exclude any effect of repetition and (2) to generalize our results to natural images (i.e. our effect is not related to the use of highly homogenous cropped faces). Indeed, the effect of repetition or the effect of habituation may dramatically impact both neural and behavioural response. For example, in a previous study proposed by Seeck et al. (1997), the authors reported differential activity starting as fast as 50 ms post-stimulus onset when subjects had to recognize a picture presented before. In this kind of task, early effects are likely accounted for by habituation of low-level features of the pictures. On the contrary, the current study aimed at testing familiarity for famous persons presented in pictures never seen before by the subjects. Thus, subjects have to recognize the person (involving long term memory retrieval) rather than the picture. We suggest that the use of unrepeated and natural stimuli concomitantly with speed constraints explains our result (i.e., early modulation of the N170).

A complementary single-trial temporal decoding analyses provided some more insights into the dynamics of face recognition as the N170 differential effect appears to be related to a first transitory phase (transitory bump of decoding power) starting at around 140 ms, which, however, returned to baseline afterwards. In addition, the N170 modulation was related to behaviour. Subjects presenting the largest N170 modulation by familiarity showed an early peak of fast behavioural responses and tended to be faster than the subjects showing less N170 modulation. Actually, the group of subjects showing less N170 modulation showed higher accuracy (and delayed RTs). Importantly, the knowledge about famous faces (post-experiment ratings) did not differ between Group 1 and Group 2 suggesting that these two groups did not differ in their ability to recognize people. We can hypothesize that the differences observed may be due to the use of different strategies. Subjects of Group 1 may base some of their response on an early representation of familiarity which is at this stage, very coarse and lead to a larger number of errors (i.e. higher number of false alarms) and thus lower accuracy, whereas subjects from Group 2 only use belated, more refined, representation of familiarity. Indeed, in two previous behavioural studies (Barragan-Jason et al., 2012, 2013), we showed that some subjects were spontaneously faster than others (100 ms faster) in a rapid go no go task similar to the one we used in the current study. In addition, an extra-analysis comparing the decoding power for the fastest trials (< median RT) and the slowest trials (> median RT) regardless of group revealed that EEG activity related to the fastest trials was decoded during the N170 time window (i.e., 145 ms). Furthermore, this early familiarity process doesn't seem to be used by all participants. Indeed, RT distributions clearly show a shift to the right for Group 2 even for their fastest responses. However, a previous behavioural study showed that if we use even more stringent speed-constraints (Speed and Accuracy Boosting procedure: SAB), it seems possible to constrain most subjects to use the fastest strategy (Barragan-Jason et al., 2013). All in all, our view is thus that our results reveal that there is a potential for an early familiarity mechanism that could be used in certain circumstances: e.g. very fast recognition or recognition of highly well-known faces such as those of kinship. Some subjects would spontaneously use this fastest strategy most of the time, while others would use it with more variability. Using even more stringent speed-constraints (Barragan-Jason et al., 2013; Besson et al., 2012) could be very interesting in this context in order to test the hypothesis that reliance on the putative familiarity processes indexed by the N170 could be increased in some conditions.

4.2. *A massive familiarity effect after 200 ms?*

We also report a familiarity effect on the N250, as soon as 200 ms after the stimulus presentation (point-by-point analysis and MVPA, Fig. 3), that is consistent with previous studies (e.g. Bentin and Deouell, 2000; Eimer et al., 2012; Kaufmann et al., 2009; Tanaka et al., 2006), although here we focus on the onset of this activity. MVPA revealed that this activity is not transitory but that the decoding power keeps increasing after 200 ms (Fig. 3C). Indeed, it can be argued that the N250 reflects not one, but several processes taking place during the period when familiarity with a given face emerges. Actually, familiarity has started to be described not as a single process, but as reflecting a cascade of subprocesses (Besson et al., 2014; Dienes et al., 2011; Whittlesea and Williams, 2000). First, familiarity requires face processing at the exemplar level (Scott et al., 2006; Tanaka et al., 2006). Second, familiarity requires access to memory, i.e. to some internal representation signalling that the face has already been seen. Third, familiarity is a more or less strong “sense” of familiarity (e.g. the butcher-on-the-bus phenomenon; Yovel and Paller, 2004) related to decisional processes (Philiastides and Sajda, 2006). Last, but not least, explicit familiarity requires that the subject be aware of this familiarity (e.g. “noetic consciousness” Tulving, 1985; or access to a “global neuronal workspace” Dehaene and Changeux, 2011 for a review). All these processes, and possibly others, may sum up during the N250 time-course.

However, go/no-go tasks, although very useful to study fast processes, have limits when making interpretations and conclusions about the role of late familiarity effects. Indeed, since we used a go/no-go paradigm, it is difficult to disentangle whether the differential activity observed during the N250 (from 200–350 ms) or the massive increase of decoding power found after 200 ms reflect a motor, rather than a familiarity effect. It is well known that go/no-go tasks elicit a systematic N2 at similar latencies to the N250 (Eimer, 1993; Gajewski and Falkenstein, 2013). The recent study of Caharel et al. (2014) using a similar go/no-go paradigm report that the N250-indexed familiarity and was related with behaviour. But, since they report RTs as fast as 280 ms (due to the repetition of stimuli that boosted RTs) and given that about 100–130 ms are needed for decision and motor responses (Kalaska and Crammond, 1992; Vanrullen and Thorpe, 2001), it is possible that the neural effect they found between 200 and 300 ms was largely contaminated by motor responses. In contrast, the results presented in Fig. 4 revealed a motor effect on the N250a and the N250b. However, the subjects who performed a categorization task in the previous study presented RTs (both minimum RTs or median RTs) about 180 ms faster than in the current study. Therefore, this comparison is very conservative and suggests that any effect of motor activity in our study occurs even later than the N250b time window. In addition, early effect of familiarity is very unlikely to be affected by motor responses that only start at 460 ms (minimal RT at 390 ms for the fastest subjects) in our task. The analysis of motor effect (Fig. 4) thus confirms that the fast familiarity effect occurring during the N170 time-window is not contaminated by motor activity.

Considering the fact that some of the subjects did not use this early familiarity (i.e. no N170 modulation) but did perform the task, our results strongly suggest that neural processing taking place as fast as 140 ms are involved in early familiarity for unrepeated familiar faces but also suggest that rather than a simple single-process, familiarity for faces is a more complex phenomenon that may also imply a cascade of neural processes occurring right after this time, i.e. during the N250 time-window.

4.3. *Spatio-temporal dynamics of face recognition*

Three models of the spatio-temporal dynamics of face recognition can be schematized (Fig. 7). A first possibility is that familiarity for faces emerges concomitantly with the activation of the posterior areas of the visual ventral stream involved in the generation of the N170 (Fig. 7A). This set of areas could encompass the Occipital Face Area (OFA) and the Fusiform Face Area (FFA). Indeed, the model proposed by Haxby et al. (2000) suggested that perception of unique identity could result from the activation of the core network. Furthermore, the FFA and OFA show an adaptation effect for identity and could therefore be involved in representing individual faces (e.g. Ishai et al., 2002; Kriegeskorte et al., 2007; Parvizi et al., 2012; Rossion, 2008).

However, this concept runs counter to the idea that selectivity is higher at the top of the visual hierarchy, whereas face familiarity requires the highest level of selectivity. Furthermore, Hochstein and Ahissar (2002) have suggested that “vision-with-scrutiny” of the type required to identify a face could be based on processes beginning at the top of the visual hierarchy. Many studies (e.g. Aggleton and Brown, 1999) further suggest that anterior visual ventral areas are necessary to compute familiarity signals. Intracranial EEG recordings have consistently found prominent activity evoked by face recognition tasks in these areas, such as in the perirhinal cortex and the amygdala, or robustly in the hippocampus, which sits at the top of this hierarchy (Barbeau et al., 2008; Dietl et al., 2005; Trautner et al., 2004). This is also in keeping with the fMRI studies in both animals and humans that have identified more patches of activity that respond to individual faces or identity in anterior than in posterior temporal lobe areas (Freiwald and Tsao, 2010; Kriegeskorte et al., 2007; Rajimehr et al., 2009; Rotshtein et al., 2005). Another model of familiarity for faces is thus that face familiarity requires the mandatory activation of anterior areas, which would translate in longer neuronal latencies (Fig. 7B).

Lastly, an alternative model (Fig. 7C) is that familiarity for faces can emerge at different stages of the visual ventral stream depending on the stimuli (robustly encoded or not, see Tong et al.,

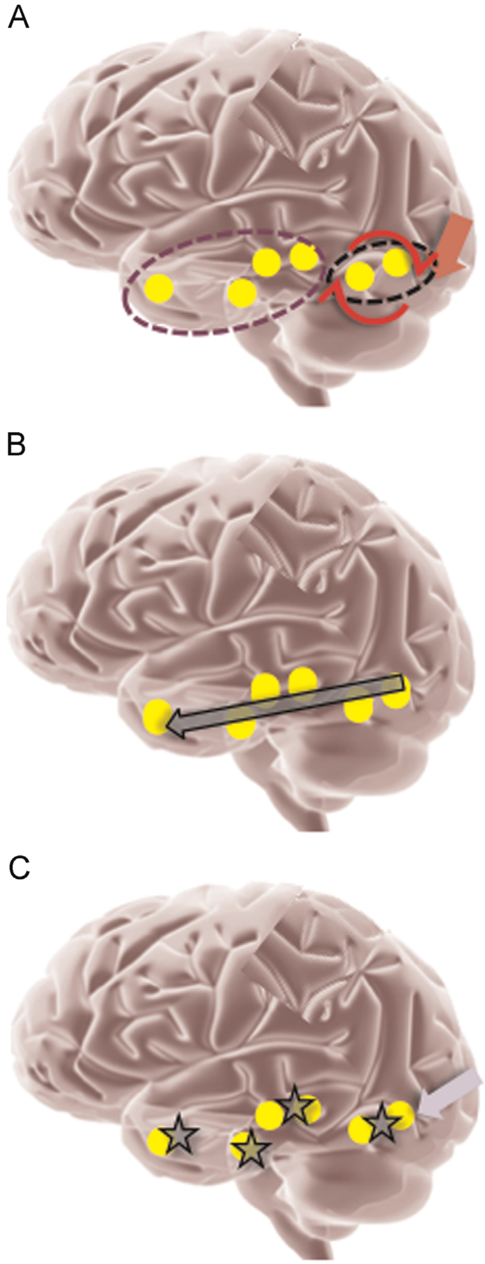

Fig. 7. Schematized models of familiarity for faces. (A) familiarity for faces emerges from the activation of posterior areas and could occur rather early (around the N170). The black circle schematized the cortical face network (fusiform face area (FFA) and Occipital face area (OFA) described by Rossion (2008). The purple circle represents the area involved in memory such as the hippocampus, the parahippocampal regions and the temporal pole (B) familiarity for faces requires the activation of areas at the top of the visual ventral stream hierarchy, areas that could be critical for selectivity and familiarity signals. In this case, familiarity would occur later than the activation of posterior areas (e.g. around the N250)**.** The arrow represents the ventral pathway. (C) familiarity for faces can emerge at different stages of the visual ventral steam depending on stimuli and tasks.

2000), tasks (fast or not) or strategy of the subjects (e.g. liberal vs conservative bias; familiarity vs identity-based recognition). We believe it is useful to conceptualize these models as they can then be tested, and eventually discarded, in future studies using either M/EEG or fMRI. The results of the present study clearly favour model C.

In conclusion, our study provides useful time limits that may be applied to constrain models of face recognition. Our results suggest that the N170 could play a role in famous face recognition, particularly in fast recognition of famous faces. Importantly however, the current study suggests that familiarity for faces is a complex phenomenon that may imply a cascade of neural processes. Additionally, we illustrate how MVPA can be efficient for reading out evoked potentials without any a priori on the components or electrodes of interest. The use of even more stringent time-constraints (Barragan-Jason et al., 2013) will be very useful to assess more precisely the role of the N170 in face familiarity.

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