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Published online: 16 Jun 2015.

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Temporal dynamics of the face familiarity effect: bootstrap analysis of single-subject event-related potential data

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Prior event-related potential studies using group statistics within a priori selected time windows have yielded conflicting results about familiarity effects in face processing. Our goal was to evaluate the temporal dynamics of the familiarity effect at all time points at the single-subject level. Ten subjects were shown faces of anonymous people or celebrities. Individual results were analysed using a point-by-point bootstrap analysis. While familiarity effects were less consistent at later epochs, all subjects showed them between 130 and 195 ms in occipitotemporal electrodes. However, the relation between the time course of familiarity effects and the peak latency of the N170 was variable. We concluded that familiarity effects between 130 and 195 ms are robust and can be shown in single subjects. The variability of their relation to the timing of the N170 potential may lead to underestimation of familiarity effects in studies that use group-based statistics.

Keywords: face perception; familiarity; temporal dynamics; bootstrap; electroencephalography

Familiar faces can be recognized more accurately and faster than unfamiliar faces even under poor viewing conditions (see e.g., Bruce, Henderson, Newman, & Burton, 2001; Burton, Wilson, Cowan, & Bruce, 1999; Sinha, Balas, Ostrovsky, & Russell, 2006; Tong & Nakayama, 1999). The timing of the emergence of the neural processes that underlie this complex perceptual task is still not well understood. Previous studies have examined these mainly by using event-related potentials (ERPs), an electroencephalographic technique with high temporal resolution. The typical strategy has been to look for differences

associated with viewing familiar versus unfamiliar faces in the amplitude of particular ERPs during specific time windows. However, these studies have not produced consistent results. Some reports found early face familiarity effects between 140 and 180 ms (during the N170 component) (Caharel, Courtay, Bernard, Lalonde, & Rebai, 2005; Caharel, Fiori, Bernard, Lalonde, & Rebai, 2006; Caharel et al., 2002; Harris & Aguirre, 2008; Kloth et al., 2006; Marzi & Viggiano, 2007; Todd, Lewis, Meusel, & Zelazo, 2008; Wild-Wall, Dimigen, & Sommer, 2008), but not others (Bentin & Deouell, 2000; Eimer,

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2000; Rossion et al., 1999), while yet others reported late face familiarity effects between 235 and 335 ms (N250 component; Tanaka, Curran, Porterfield, & Collins, 2006).

Some of these discrepancies may be attributable to differences in experimental design, such as the type of familiarity of the faces used (e.g., personally familiar faces, in contrast to famous faces, may provide a richer face representation that encompasses not only visual but also strong emotional information). A less considered but equally important source of discrepant results may be the method of analysis. Two factors may be of particular concern. First, most previous reports contrasted peak or mean amplitude values over temporal windows that were selected a priori to include components such as the N170, which consistently show "face-sensitivity" (i.e., significant amplitude differences in response to faces compared to other objects). However, it is not logically necessary that the time periods when the neural signals generated by viewing faces and viewing objects differ the most will also be the periods when differences between familiar and unfamiliar faces will occur. Second, traditional ERP analysis relies on group statistics, by using as input the average data of individuals for each experimental condition and then comparing the effects of condition at a group level. These do not take into account individual differences in the timing of the emergence of familiarity effects and may potentially obscure interesting effects with dynamics that vary between single subjects constraining the range of conclusions possible.

To overcome such limitations, a major goal of this study was to implement an analytic method to study the electroencephalographic activity generated by familiar and unfamiliar faces time point by time point at the individual subject level. Such an analysis would be free of a priori assumptions about the particular time at which familiarity effects emerge and would still be sensitive to differences despite slight temporal variations in effects across subjects. The bootstrap technique is a statistical tool particularly suited for this kind of analysis. It creates a sampling distribution for the statistic of interest (e.g., mean) by resampling from the raw data (e.g., the amplitude values obtained at a particular time point in each trial) with replacement a large number of times (Efron & Tibshirani, 1994; Wilcox, 2005; Wilcox & Keselman, 2003). This sampling distribution can be used for hypothesis testing (Oruc et al., 2011). The bootstrap technique has been successfully used in ERP studies, for example, to establish the reliability of the locations of maxima in individual topographical maps (Fabiani, Gratton, Corballis, Cheng, & Friedman, 1998), to determine the time at which the face sensitivity of particular components appears (Rousselet, Husk, Bennett, & Sekuler, 2008), to permit statistical inferences about the presence or absence of face-sensitivity of the N170 in single patients (Dalrymple et al., 2011), and to generate ERP amplitude confidence intervals from two subgroups of subjects (Caryl, Golding, & Hall, 1995). Therefore, in order to determine the presence of familiarity effects during the time window of the N170 component at the individual level, we implemented a point-by-point bootstrap technique, in which familiar and unfamiliar face viewing are compared at the individual level and at each selected electrode.

Although a valuable aspect of this method is that it is agnostic about when and where face familiarity effects will emerge, we considered an initial hypothesis. We hypothesized that the human face perception system can differentiate between familiar and unfamiliar faces as early as 130 ms. This hypothesis is suggested by several previous findings. First, neurons in nonhuman primate inferotemporal cortex accumulate information about individual faces around 40–50 ms after information about the global category of faces have been coded (Matsumoto, Okada, Sugase-Miyamoto, Yamane, & Kawano, 2005; Sugase, Yamane, Ueno, & Kawano, 1999) and have an average onset latency of about 100 ms (Tovee & Rolls, 1995). Second, adaptation studies in humans show that the amplitude of the face-sensitive N170 component (130–180 ms) is reduced for identical faces compared to faces of different people (Jacques & Rossion, 2006, 2007). Third, humans can discriminate faces behaviourally around 200 ms (Jacques & Rossion, 2007).

Method

Subjects

Ten healthy subjects (five males, mean age 28.1 ± 3.57 years, all right-handed) participated in the study. All subjects had normal or corrected-to-normal visual acuity. The institutional review boards of Vancouver General Hospital and the University of British Columbia approved the protocol, and all subjects gave informed consent in accordance with the declaration of Helsinki.

Stimuli

We used images of faces slightly smiling or with neutral expression, without identifying accessories (e.g., glasses) and with only minimal hair visible (Figure 1). All images were sized to 400 pixels in width with a resolution of 300 pixels per inch. Four images were obtained for each of five different people in the two categories, familiar faces (pictures of celebrities) and unfamiliar faces (pictures of individuals unknown to the subjects). The small number of different identities in each category was used to avoid differences among the familiar faces in terms of degree of familiarity: The smaller the stimulus set, the higher the chances that all faces were equally familiar to all subjects. This was an important aspect to control for because even small differences in terms of degree of familiarity could have led to a decrease in the strength of the familiarity effect across trials pertaining to that condition. Variation in viewpoint from frontal to three-quarter view as well as slight differences in face sizes were used to minimize possible familiarity effects based on perceptual processing of visually identical retinal images (Figure 1).

Several measures were taken to minimize possible differences in low-level visual properties between the two picture sets (i.e., familiar and unfamiliar faces). First, the original pictures were converted to grey scale and were approximately equated for luminance and contrast using the SHINE toolbox (Willenbockel et al., 2010). We confirmed that there was no significant difference between the mean luminance of the familiar and unfamiliar face stimuli based on an independent-samples *t*-test (mean luminance = 8.74 ± 1.94 cd m^{-2} for familiar; 8.70 ± 4.91 cd m^{-2} for

unfamiliar), $t(38) = 0.03$, $p = .98$. Similarly, there was no difference between average root mean square (RMS) contrast of the two stimulus sets (mean RMS contrast = 1.14 ± 0.16 for familiar and 1.28 ± 0.32 for unfamiliar), $t(38) = -1.81$, $p = .08$.

In addition, we performed a pilot study to determine whether we could detect effects due to low-level visual properties, by presenting the original pictures not equated for contrast and luminance to a different group of 11 subjects (mean age 28 ± 10.12, three males, 9 right-handed). All aspects of the experimental procedure, electroencephalographic recording, and data analysis were similar to those of the actual experiment (described in detailed in the next sections) except that they were not warned in advance about whose faces they were going to see. On these data, we performed a point-by-point comparison using the bootstrap technique (see next section for further details on this technique) focusing on the P1 component. This component is a positive peak that reaches its highest amplitude between 80 and 120 ms at occipital and occipitotemporal electrodes. Previous face perception studies have shown that P1 amplitude modulations disappear (Rossion & Caharel, 2011) or are weak in amplitude, scattered in time, and present in only a small minority of observers (Rousselet et al., 2008) once low-level properties are matched. Therefore, we reasoned that stimuli that differ in low-level properties should generate significant differences during the time window of this early P1 component, and that these P1 differences should be eliminated if the stimulus set is successfully equated for low-level properties. If the latter was achieved, then differences in later epochs would probably not be due to effects of low-level properties.

Procedure

A preexperimental questionnaire confirmed that all participants recognized the familiar faces and did not recognize the unfamiliar faces. This part of the protocol may also have enhanced our findings, as some authors have suggested that the N170 familiarity effect is more consistently observed if subjects know in advance the faces that are going to be presented (Caharel, Ramon, & Rossion, 2014).
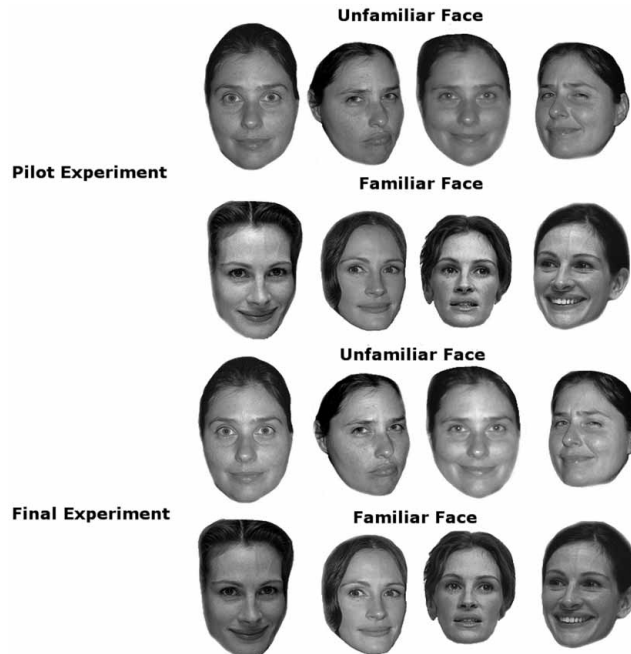
Figure 1. Examples of the faces used for both the pilot and the final experiment.

Subjects were seated in a sound-attenuated room, 100 cm from a 17″ computer monitor. The experiment was programmed and carried out using MATLAB (Mathworks) and PsychToolbox (Brainard, 1997). Each trial began with a black fixation dot at the centre of the screen. Between 2700 and 2900 ms later a face, selected randomly from the familiar or unfamiliar categories, appeared for 100 ms. It was followed by a 300-ms visual mask. The next trial began with the reappearance of the fixation point. Subjects were instructed to indicate whether the images they saw were pleasant or unpleasant, by pressing a button on a video game controller as soon as possible. The response hand was counterbalanced across participants. This task was irrelevant to the purpose of the study and was implemented to ensure that subjects attended to the screen. There were 200 trials for each of the two categories, presented in a random order.

Electrophysiological recording

Brain electrical activity was recorded using a standard 64-electrode cap (Biosemi Active 2 system) and five additional electrodes (three eye movement channels plus the two mastoids). All recordings were performed relative to two scalp electrodes located over medial parietal cortex (CMS/DRL), amplified with a gain of 0.5 and digitized online at a sampling rate of 256 samples per second. Offsets at each active electrode, which are a running average of the voltage measured between CMS and each active electrode and reflect the half-cell potential of the electrode/gel/skin interface, were kept between ±40 mV at rest. Vertical eye movements were recorded using an electrode inferior to the right eye, while horizontal eye movements were recorded using electrodes on the right and left outer canthi.

Analysis

First, the data were visually inspected, and channels that were particularly noisy were identified, removed, and later interpolated using spherical splines as implemented in EEGLAB (Delorme & Makeig, 2004). Each subject's signal was then algebraically transformed to average reference

and low-pass filtered with a Butterworth filter (25.6 Hz half amplitude cut-off).

The bootstrap analysis of single-subject data was focused on a set of electrodes that, according to previous studies, exhibit the strongest and most consistent response to different types of visual stimuli, including faces. Those electrodes were: (a) P1/P2, P3/P4, P5/P6, P7/P8, P9/10, PO3/PO4, PO7/PO8, Pz, POz, where the face-selective component N170 (see, for example, Jacques, d'Arripe, & Rossion, 2007) as well as the N250 (see, for example, Tanaka et al., 2006) are most prominent; (b) O1/O2 and Oz, where early visual components (e.g., P1) usually reach their highest amplitude (see, for example, Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002); (c) CPz, Cz, Fz, FCz, FT7/FT8, FC5/FC6, FC3/FC4 and FC1/FC2, C1/C2, CP1/CP2 where the positive counterpart of the N170, the VPP (Jeffreys, 1989, 1996; Joyce & Rossion, 2005; Schendan, Ganis, & Kutas, 1998), reaches its highest amplitude.

After each subject's data were preprocessed, trials were separated into the two categories of familiar and unfamiliar faces. Amplitude values were extracted at 4-ms intervals (corresponding to the sampling rate of the electroencephalography (EEG) equipment used) from 0 to 400 ms after stimulus onset (baseline correction was performed by subtracting the average amplitude over 100 ms of prestimulus activity from each time point). At each time point there was a data set of 200 amplitude values (one value for each of the 200 trials) for each of the two conditions for that subject. The bootstrap procedure resampled the data for a given time point with replacement 10,000 times. The average of each new resampled data set for familiar faces was subtracted from the mean of the new resampled data set for the unfamiliar faces. A histogram of these 10,000 differences between means was then created for each time point and each electrode separately. The lower and upper 2.5th percentile points of the histogram served as the critical values for two-tailed significance at the .05 level (see Oruc et al., 2011, for further details on the implementation of this method). A significant familiarity effect was one where the value 0 (i.e., no difference) lay outside these 2.5th percentile points for the subtraction

between familiar and unfamiliar conditions. For each subject we corrected for multiple comparisons using the Bonferroni correction adjusted for interitem correlations (Sankoh, Huque, & Dubey, 1997). Note that this analysis is performed for each electrode individually, thus 100 bootstrap analyses per electrode, per subject were performed.

Results

ERP components

We first inspected the ERP response obtained from each individual subject to identify potentials denoted in earlier studies that have used a similar methodology (see, e.g., Rossion & Jacques, 2011; Tanaka et al., 2006). We identified the P1 component as the most positive peak in the interval 80–120 ms, the N170 as the most negative peak in the interval 130–190 ms, the P2 as the most positive peak in the interval 190–275 ms, and the N250 as the negative deflection in the interval 235–335 ms.

Components P1, N170, and P2 were observed in all 10 subjects. P1 reached its largest amplitude in occipital electrodes O1 and O2. N170 and P2 reached their largest amplitude in occipitotemporal electrodes (P7/P8, P9/P10, and PO7/PO8). Following component P2, a negative deflection, identified as the N250, was observed in six subjects. It reached its largest amplitude also at occipitotemporal electrodes (P7/P8, P9/P10, and PO7/PO8; Figure 2).

The pilot experiment: Effects of matching luminance and contrast

Using the pilot face stimuli that were not matched in luminance and contrast, we found that between 80 and 130 ms, a period that coincided with the P1 component (Figure 3), differences between the familiar and unfamiliar sets appeared in three subjects in left occipitotemporal electrodes (P7, P9, and PO7), in eight subjects in occipital electrode O1. They also appeared in between one and eight subjects in right occipitotemporal electrodes (P8, P10, and PO8) and in six subjects in occipital electrode O2. In contrast, in the main experiment, in which luminance and contrast was matched across
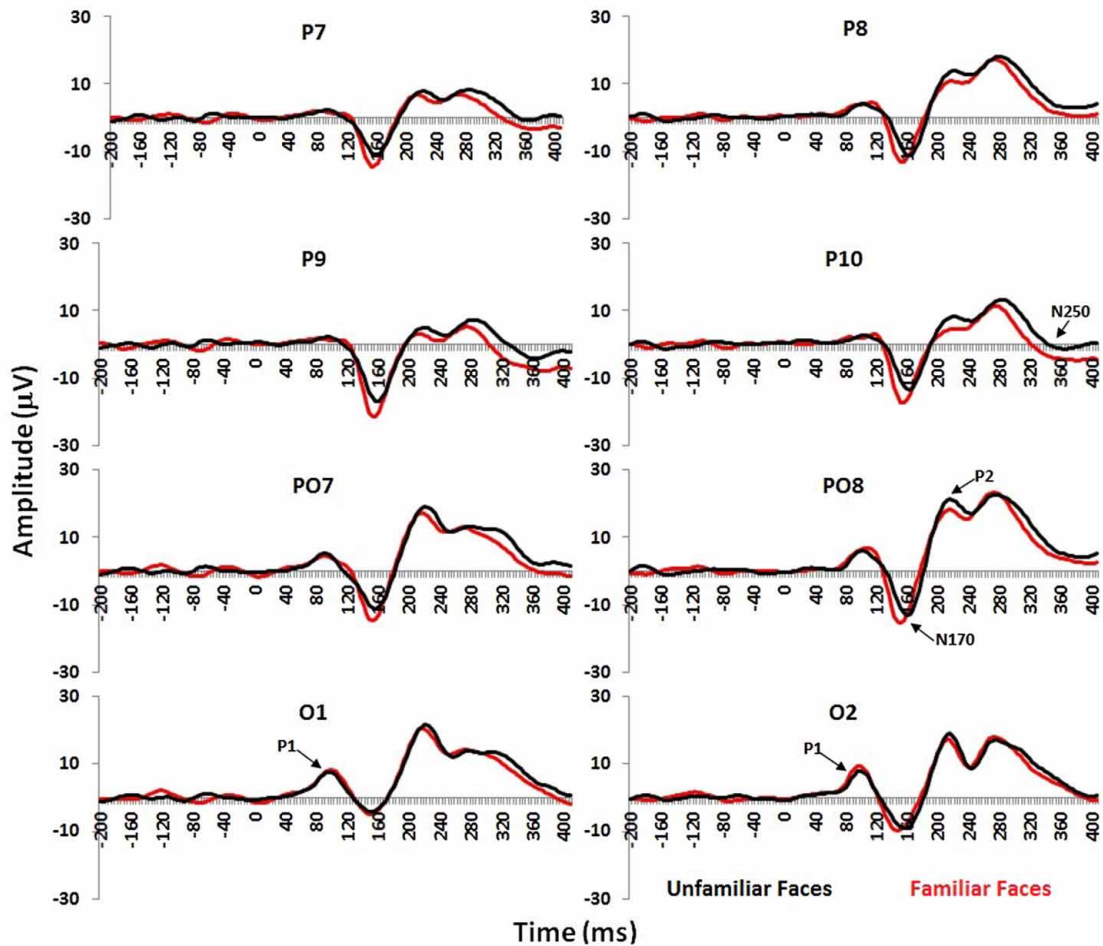
Figure 2. Averaged event-related potential (ERP) waveforms in response to familiar (red trace) and unfamiliar (black trace) faces in one representative participant. Components P1, N170, P2, and N250 components are indicated in the electrodes where they were most clearly observed. [To view this figure in colour, please see the online version of this Journal.]

the familiar and unfamiliar sets of faces (see Method), this early P1 effect was nearly eliminated, appearing only during scattered time points in three subjects: S01 showed P1 differences in electrodes PO7/PO8 and O1/O2, S05 only in PO8, and S10 only in P8 (Figure 3).

Main experiment: Bootstrap results for familiarity effects

We first determined the electrodes that exhibited the largest number of time points at which significant

differences between familiar and unfamiliar conditions were detected across subjects. Considering that we had 100 time points (from 0 to 400 ms after stimulus onset with a 4-ms time resolution) and 10 subjects, the maximum number of time points for any given electrode was 1000. The highest ranked electrodes were P7/P8, P9/P10, PO7/PO8, and Pz (Figure 4), which, apart from Pz, were also those with the largest N170, P2, and N250 components.

After selecting these as electrodes of interest, we determined when significant differences between conditions appeared for each subject. Significant
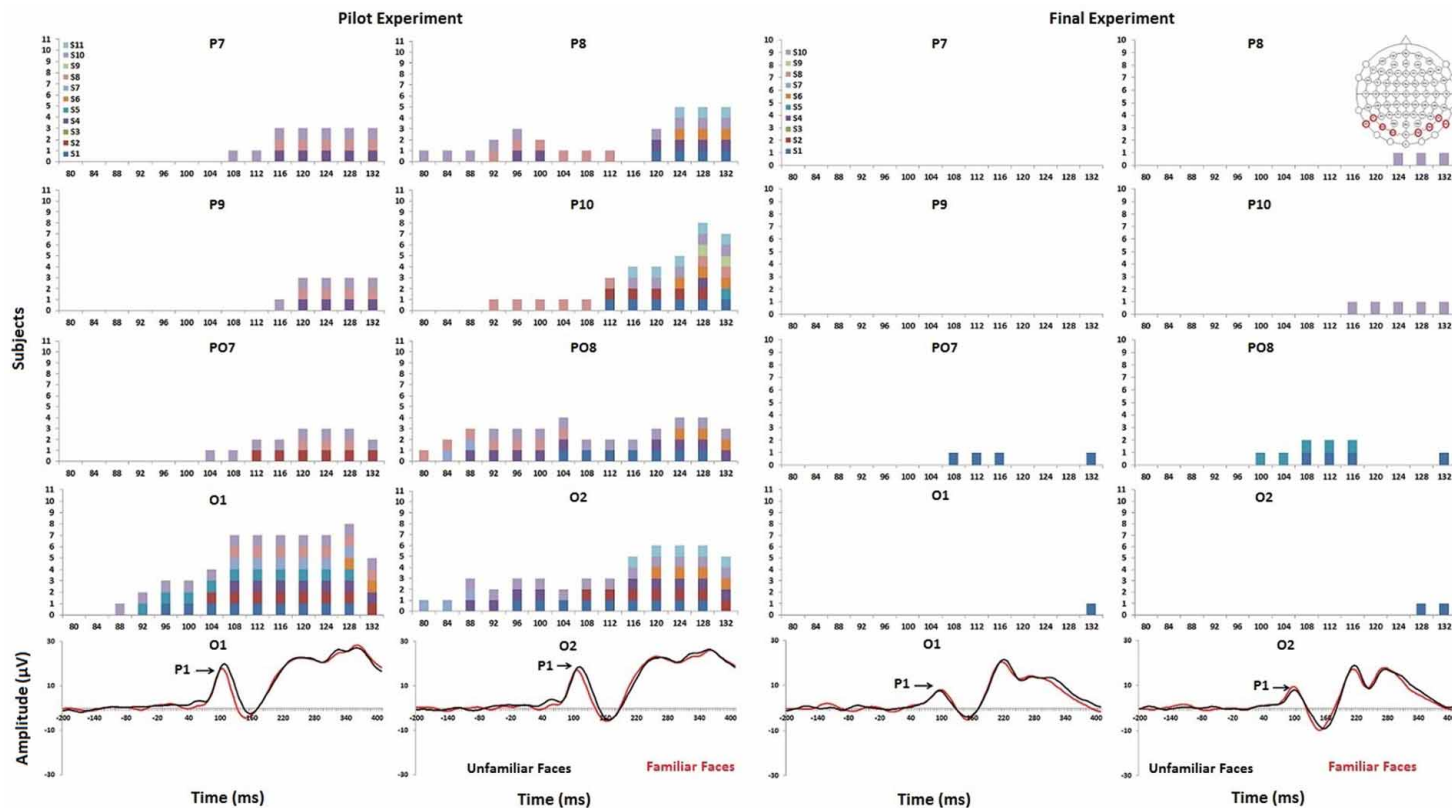
Figure 3.   Differences between familiar and unfamiliar faces during the time window of the P1 component when the stimulus low-level properties were not equated (pilot experiment) and when they were equated (final experiment). For occipitotemporal and occipital electrodes, significant time points (80–130 ms) for familiarity effects are depicted as bars on a raster line. The bar colours indicate different subjects. Note that significant differences are more consistently observed when the stimulus low-level properties were not equated (pilot experiment). In the final experiment, for which such properties were equated across both stimulus sets, the differences between conditions are infrequent and scattered. Red circles indicate the scalp location of the electrodes of interest. [To view this figure in colour, please see the online version of this Journal.]
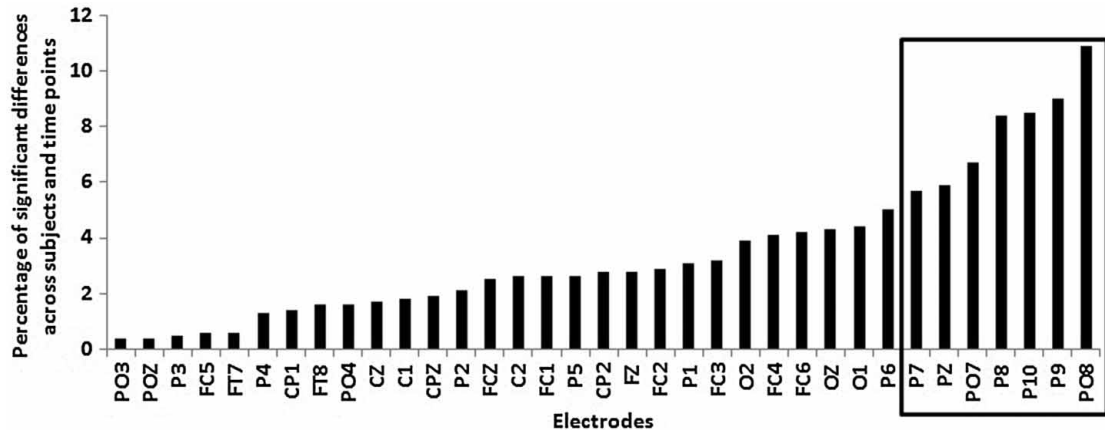
Figure 4. Percentage of significant differences found between familiar and unfamiliar face conditions across subjects and time points. Note that electrodes P7/P8, P9/P10, PO7/PO8, and Pz presented the highest amount of time points during which differences in the brain response to familiar and unfamiliar faces were found.

familiarity effects in electrode Pz were variable and only brief in six subjects: Its high ranking above was due to one anomalous subject (S02) with prolonged late familiarity effects from about 260 ms onwards (Figure 5). Hence, to simplify our analysis, we limited further consideration of familiarity effects to P7/P8, P9/P10, and PO7/PO8.

The most consistent familiarity effects were found between 130 and 195 ms, coinciding with the N170 component. All 10 subjects showed familiarity effects in the right hemisphere and eight subjects in the left (Figure 5). Specifically, S01, 02, 04, 05, and 07 presented bilateral differences in all occipitotemporal electrodes of interest. S03, 06, 08, 09, and 10 presented differences in at least one occipitotemporal electrode in the right hemisphere, while S06, 08, and 09 also presented differences in at least one occipitotemporal electrode in the left hemisphere. Differences in right occipital electrode (O2) were observed in S01, 02, 03, 04, 05, 07, and 08. In the equivalent left-hemisphere electrode (O1) differences were observed in S01, 02, 05, 06, and 07 (Figure 5).

Later effects were more inconsistent. During the time window of the P2 (190–275 ms), three subjects showed familiarity effects in both hemispheres (S01, S02, S04), and one in the right hemisphere (S09; Figure 5). From 275 to 335 ms, during the time window of the N250, three subjects (S04, S07, and S10) showed familiarity effects in both

hemispheres, while one (S01) did in the right hemisphere only (Figure 5).

Relation between familiarity effects and the N170 component

The most consistent familiarity effects in our subjects thus appear to coincide with the time window of the N170 component. To better characterize the temporal relation between the N170 and familiarity effect in each subject, we noted the timing of the N170 peak amplitude and the beginning and end of the interval over which familiarity effects were found. The onset and offset of the familiarity effect in the 130–195-ms window in any of the P7/P8, P9/P10, and PO7/PO8 electrodes was taken as the first appearance of a significant difference between familiar and unfamiliar conditions. The peak of the N170 in each subject was taken from a waveform averaged over the P7/P9/PO7 for the left and P8/P10/PO8 for the right hemisphere.

In four subjects (S04, S05, S07, and S08) the familiarity effect overlapped with the N170 peak (Figure 6). In the right hemisphere the familiarity effect began 11 ± 8.25 ms before the N170 peak for familiar faces and ended 24 ± 8.64 ms after, and began 23 ± 13.22 ms before the N170 peak for unfamiliar faces and ended 12 ± 11.78 ms after. In the left hemisphere, it began 10.00 ± 4 ms before the N170 peak to familiar faces and ended
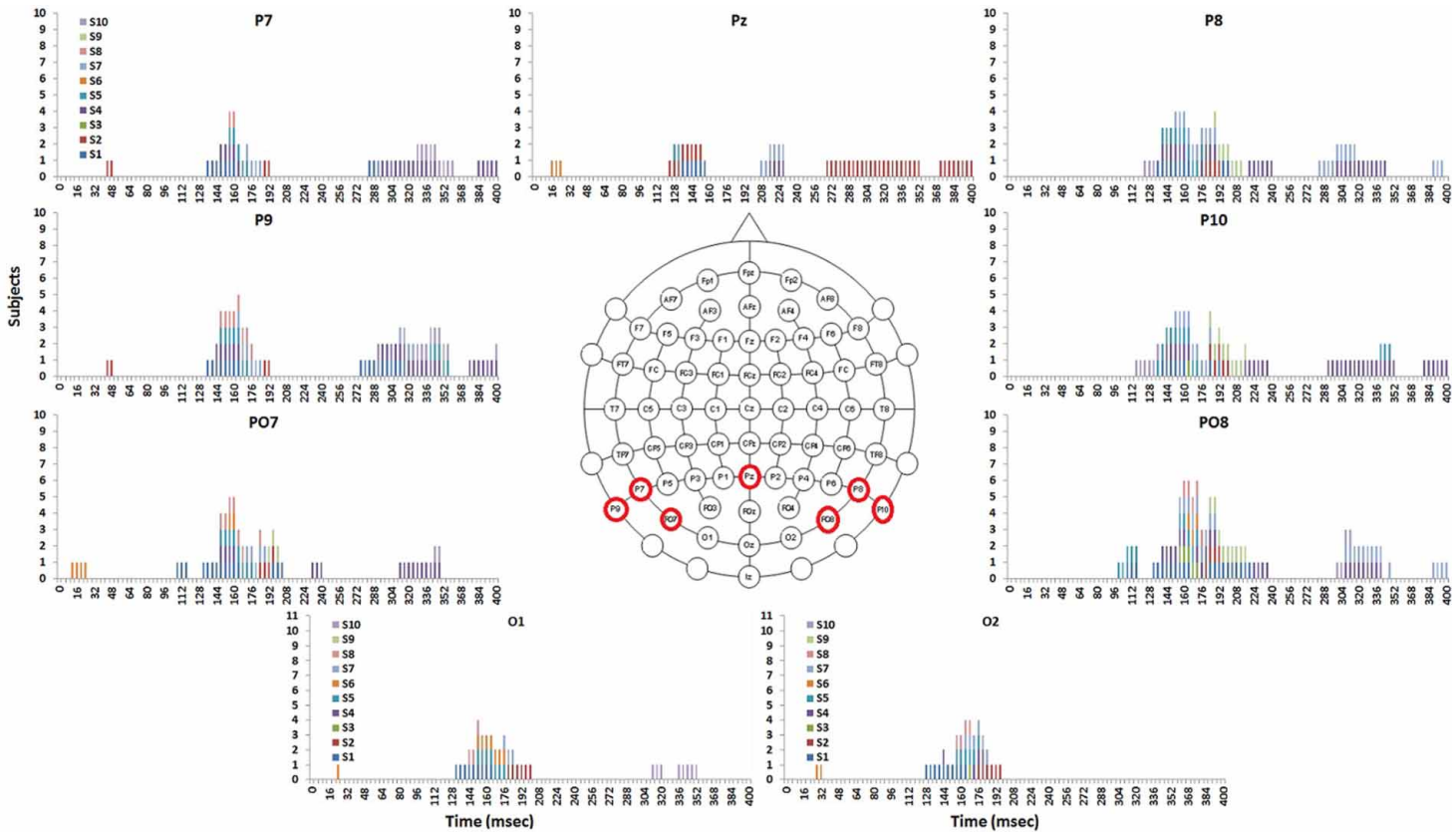
Figure 5.   Individual bootstrap results: Each subject's significant time points for familiarity effects depicted as bars on a raster line. The bar colours indicated different subjects. Red circles indicate the scalp location of the electrodes of interest. Note that the differences were most consistently observed across subjects between 130 and 195 ms. [To view this figure in colour, please see the online version of this Journal.]
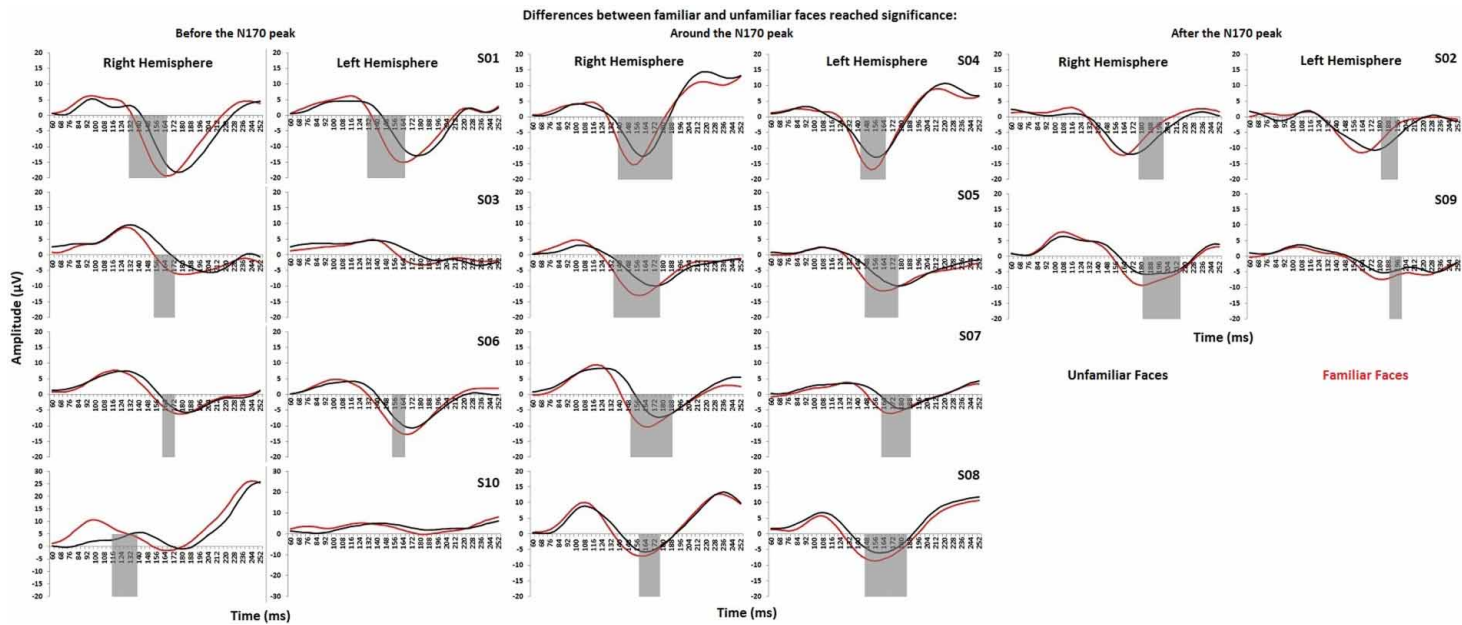
Figure 6. Temporal relation between the start and end of the familiarity effect and the N170 peak for each individual subject. For each participant, waveforms are presented from 60 to 250 ms. Time intervals during which the difference between both waveforms reached statistical significance are indicated in grey. Subjects are grouped according to three patterns of temporal relation between the familiarity effect and the N170 peaks (see text for further details). [To view this figure in colour, please see the online version of this Journal.]

17 ± 7.57 ms after, and began 18 ± 9.52 ms before the N170 peak to unfamiliar faces and ended 9 ± 11.49 ms after.

However, in four other subjects (S01, S03, S06, and S10) the familiarity effect ended before the N170 reached its peak. In the right hemisphere, it ended 13 ± 12.81 ms before the N170 peak for familiar faces and 25 ± 17.70 ms before the N170 peak for unfamiliar faces. In the left hemisphere, a familiarity effect was seen only in two of these four subjects, S01 and S06. In S01 it ended at the same time as the N170 peak to familiar faces and 12 ms before the peak to unfamiliar faces, while in S06 it ended 8 ms before the N170 peak to familiar faces and 12 ms before the N170 peak to unfamiliar faces.

Finally, in two subjects (S02 and S09) the effect began after the N170 peak. In the right hemisphere, S02 had a familiarity effect that began 16 ms after the N170 peak to familiar faces and 8 ms after the N170 peak to unfamiliar faces, while in S09 it began 4 ms after the N170 peak to familiar faces and at the same time as the N170 peak to unfamiliar faces. In the left hemisphere, in the familiarity effect began 20 ms after the N170 peak to familiar faces and 8 ms after the N170 peak to unfamiliar faces, while in S09 it began 12 ms after the N170 peak to familiar faces and 8 ms after the N170 peak to unfamiliar faces.

Inspection of the individual traces revealed that the most consistent effect of familiarity is a shift of part or all of the N170 waveform towards earlier time points (Figure 6). Whether such a shift translates to a difference between the two curves at a particular time of the N170 potential depends on a number of factors, including the size of the shift, whether the shift affects both the descending and ascending arms of the waveform similarly or if there is a change in the width of the potential, and whether there is also a change in the amplitude of the peak, as appears to be the case in only some subjects (e.g., S04, S05, and S07).

Discussion

We used a point-by-point bootstrap analysis to study the temporal dynamics of the face familiarity effects at the single-subject level. This method avoids a priori assumptions about the temporal window of

the effect and accounts for interindividual differences. Most consistently, we found familiarity effects in all participants in occipitotemporal electrodes of the right hemisphere and in eight participants in the left hemisphere between 130 and 195 ms, coinciding with the N170 component. However, we also found that the temporal relation between familiarity effects and the peak latency of the N170 component differs between subjects, sometimes before, after, or coinciding with the peak.

Before we discuss our results, a number of technical factors deserve mention. First, we used a small number of different identities (five identities, four versions of each one). This could have two consequences: Subjects might become familiar with the unfamiliar faces over the course of the experiment, or our familiarity effects could be confounded by repetition effects. The first of these, increasing familiarity with the unfamiliar set, might have reduced the difference in familiarity effects between the familiar and unfamiliar set: If anything this would bias against the positive results we obtained. Regarding the repetition effect, previous ERP studies using a wide variety of stimuli have shown that repeated items generate more positive waveforms, but that these occur more consistently between 250 and 500 ms (Doyle & Rugg, 1998; Friedman, 1990; Mecklinger & Meinshausen, 1998; Munte et al., 1997; Nessler, Mecklinger, & Penney, 2005; Penney, Mecklinger, & Nessler, 2001; Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991; Rugg & Doyle, 1992; Rugg & Nagy, 1989), a latency value that has been replicated using faces (Jemel, Calabria, Delvenne, Crommelinck, & Bruyer, 2003; Munte et al., 1997; Nessler et al., 2005) and is later than the key familiarity effects we describe. Furthermore, the number of repetitions of each image is the same for both our unfamiliar and familiar set: Hence any repetition effect based upon image properties should be the same for both conditions. A second issue that can confound familiarity effects is the new/old or novelty effect, differences generated by the appearance of a stimulus not seen before. To guard against this, we had subjects see in advance all the faces that were going to be presented. Also, novelty effects in ERP appear about 300 to 800 ms after stimulus onset (see Friedman & Johnson, 2000; Mecklinger, 2000, for a

review; Rugg, 1995), with an early midfrontal negative ERP effect between 300 and 500 ms and a later parietal positive ERP between 400 and 800 ms (Curran, 2000; Friedman & Johnson, 2000; Mecklinger, 2000; Rugg, 1995). Thus, these novelty effects have a different topography and a longer latency later than the familiarity effects we found.

A third technical issue is whether other differences between the two stimulus sets besides familiarity could confound the results, in particular differences in low-level visual properties such as luminance and contrast. We controlled for this physically by equating both sets of face stimuli for luminance and contrast and statistically verifying that the match was successful. We then performed a pilot experiment to show that this process nearly eliminated any difference in the evoked response to the two stimulus sets in the early P1 component, which covers a period of activity highly sensitive to changes in low-level visual factors (Anllo-Vento & Hillyard, 1996; MacKay & Jeffreys, 1973; Shaw & Cant, 1980; Yiannikas & Walsh, 1983). As a consequence, we reduced the likelihood that any difference in later potentials in our main experiment with matched face stimuli were due to low-level image properties.

Face familiarity effects during the time window of the N170 component

Previous studies of face familiarity effects in the N170 have yielded conflicting results. Familiarity modulations of this component have been found with personally familiar faces, such as those of a subject's mother, their friends, or their own self (Caharel et al., 2006; Caharel et al., 2002; Kloth et al., 2006), famous faces (Caharel et al., 2006; Caharel et al., 2002) or recently learned faces associated with semantic information (Heisz & Shedden, 2009). However, this has not been replicated in other studies that have also used personally familiar or famous faces (Bentin & Deouell, 2000; Eimer, 2000; Henson et al., 2003; Jemel, Calabria, et al., 2003; Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003; Jemel, Pisani, Rousselle, Crommelinck, & Bruyer, 2005) or recently learned faces (Rossion et al., 1999). A number of factors have been proposed to explain these discrepancies

(e.g., type of face familiarity studied, number of times an unfamiliar face is presented throughout the experiment, type of task, etc.).

Our study revealed that an additional factor to consider is the intersubject variability regarding the temporal relationship between the emergence of the familiarity effect and the peak latency of the N170 component. In less than half of our subjects did the period with statistically significant differences between familiar and unfamiliar faces overlap with the N170 peak: In the rest it either preceded or followed the peak. The chief effect of familiarity appeared to be a shift of the N170 waveform to an earlier occurrence. How much of a shift occurs and whether it is accompanied by changes to the shape of the N170 potential determines when statistically significant familiarity effects will be found. These individual differences may arise from dissimilarities across subjects in nonfunctional factors such as skull thickness and cortical folding patterns, which influence the morphology of the waveforms. They may also arise from cognitive factors such as the speed at which evidence accumulates for a decision about familiarity. Regardless, this variability has methodological implications for group analyses. If the window of analysis is too narrowly centred around the N170 peak, a substantial number of subjects may not show familiarity effects in that window, reducing the sensitivity of a group-based analysis. Furthermore, our results indicate that a window focused on the ascending limb of the N170 potential has the greatest sensitivity to familiarity effects.

Familiarity effects beyond 190 ms were observed in only a minority of subjects using the bootstrap technique. This result does not exclude the possibility that familiarity effect may emerge beyond 190 ms—for example, during the N250 component—since several reasons may explain why we did not find such effects here. First, the bootstrap method is less sensitive when the component is not well differentiated (see, for example, S10 in Figure 6) or encompasses a broad waveform, which is characteristic of late cognitive potentials (Oruc et al., 2011). Second, our protocol had our subjects produce a motor response, which could have obscured the N250 and P3 components. Previous studies have shown that the P3 and N2 (the

N250 is considered part of the N2 family of negative deflections at 200–300 ms after stimulus onset, see, e.g., Warren, Tanaka, & Holroyd, 2011) are sensitive to response production. The P3 increases at parietal and decreases at the vertex and frontal electrodes when a stimuli demands a response, a "go-stimulus". Likewise, a "go-stimulus" decreases the N2 amplitude independent of the type of response (Pfefferbaum, Ford, Weller, & Kopell, 1985). The net effect of having a motor response would then be a decreased signal-to-noise ratio in these temporal windows, so that familiarity modulations are not strong enough to be detected. Indeed, problems with signal-to-noise ratio in general for these late potentials may underlie the fact that some previous studies only found face familiarity effects in the N250 potential after averaging together several channels to increase the signal-to-noise ratio (see e.g., Tanaka et al., 2006).

Conclusions

In summary, our study shows that consistent differences between familiar and unfamiliar faces can be found at the single-subject level between 130 and 195 ms. This has two implications. First, there is sufficient perceptual encoding by this time period to differentiate facial identity. Second, there is already modulation of such processing by stored information of previously seen faces at this early stage. However, the variable relationship between the N170 component and the timing of familiarity effects between subjects suggests that perceptual encoding and familiarity modulation for faces may be distinct. At a practical level, this variability highlights the value of the bootstrap technique for single-subject analyses that eliminate the need for and potential bias of a priori selection of temporal windows of analysis and has important implications for group-based analysis. First, it may provide an explanation that reconciles the mixed results of prior group analyses: Whether a significant familiarity effect is found in the N170 potential in any given study may depend upon the mix of individuals that comprise the group and the degree of homogeneity of their individual familiarity effects. Also following from this would be an important cautionary note: Heterogeneity could result in a null effect at a group level, even when familiarity effects are significant at the individual subject level.

Disclosure statement

Funding

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