



An implicit neural familiar face identity recognition response across widely variable natural views in the human brain

Xiaoqian Yan pa,b, Friederike GS Zimmermannb,c and Bruno Rossiona,b,d

^aCNRS, CRAN, Université de Lorraine, Nancy, France; ^bInstitute of Research in Psychological Science, Institute of Neuroscience, Université de Louvain, Belgium; ^aBG Klinikum Humburg, Neurologie, Hamburg, Germany; ^aCHRU-Nancy, Service de Neurologie, France

ABSTRACT

Highly variable natural images of the same familiar face celebrity interleaved periodically in a rapid (6 images/second) train of unfamiliar faces automatically elicit an objective electroencephalographic (EEG) response over the occipito-temporal cortex of neurotypical human adults within a few minutes. However, the extent to which this frequency-tagged response goes beyond the association of common physical features of the periodically repeated face identity remains unknown. Here we compare participants who know or do not know the very same periodically repeated face celebrity and show that long-term familiarity accounts for about 80% of the neural face identity recognition response. This familiarity advantage disappears with upside-down images. Variability in response amplitude between face identities is preserved for inverted faces and in unfamiliar participants, suggesting a contribution of within-person physical face variability and distinctiveness to about 20% of the face identity response. These observations provide the strongest difference to date in human brain response between the same famous face identities perceived as familiar or unfamiliar in an implicit task. The frequency-tagged neural response largely reflects the strengthening effect of long-term memory in the human occipito-temporal cortex, and may serve to index automatic familiar face identity recognition in individual observers.

ARTICLE HISTORY

Received 2 August 2019 Revised 2 January 2020 Published online 21 January 2020

KEYWORDS

Face identity recognition; frequency-tagging; inversion; EEG

Introduction

Neurotypical human adults are able to automatically recognize a familiar face identity – a family member, a friend, a foe or a celebrity – among a crowd of unfamiliar faces at a single glance. According to recent evidence, this fundamental brain function can be captured within a few minutes by presenting highly variable natural images of different unfamiliar faces at a rapid stimulation frequency, e.g., 6 images/second, with images of the same familiar face identity – a celebrity – replacing an unfamiliar face at a fixed rate (e.g., of every seventh image or 0.86 Hz) (Zimmermann, Yan, & Rossion, 2019; Figure, p. 1).

This stimulation leads to a high signal-to-noise ratio (SNR) neural response in the human electroencephalographic (EEG) frequency-spectrum exactly at 0.86 Hz and harmonics (1.71 Hz, etc.) over the occipitotemporal cortex (Zimmermann et al., 2019). This objective (i.e., frequency predefined) EEG response can be taken as a neural signature of automatic (i.e., without the intention to do so) and rapid (i.e., single-glance) familiar face identity recognition. Importantly, this neural measure is obtained across widely variable natural (i.e., unsegmented) images of faces, supporting its ecological validity

and indicating that it is not merely due to the recognition of a single iconic image of a familiar face.

An outstanding issue is whether, and if so to what extent, this frequency-tagged neural face identity recognition response is truly due to observers' long-term memory of the periodically repeated facial identity. Indeed, in this kind of paradigm (Figure 1), despite the use of widely variable images of a given face identity, a significant response could emerge solely, or mainly, from the repetition of common physical features of the periodically repeated facial identity, irrespective of its longterm familiarity. This could be particularly the case if the famous identity has a distinctive face (Valentine & Bruce, 1986) or is associated with reduced physical variability across views (i.e., within person variability, Jenkins, White, Van Montfort, & Burton, 2011) as compared to other faces presented in the paradigm. As a matter of fact, different periodically presented familiar facial identities appear to lead to substantially variable response amplitudes in this EEG paradigm (Zimmermann et al., 2019). However, the source of this variability remains unknown: it could be due to different degrees of famousness of the faces, or to physical characteristics

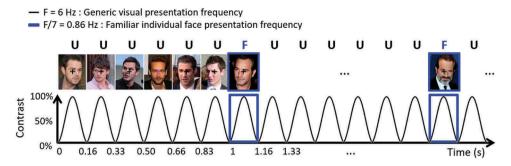


Figure 1. Schematic illustration of the experimental design used in Zimmermann et al. (2019) and in the current study. Unfamiliar faces to all of our participants (N = 28 in the current study) are repeatedly shown at 6 Hz, with a face identity familiar to only half of the participants ('familiar group') presented as every seventh image (0.86 Hz). The familiar face shown here is French actor Jean Dujardin. Face images shown here are with license permits; however, only the first, second, fifth, and sixth unfamiliar face identities were used in the current experiment. For license information, Blake Harrison, and Matt Johnson: Pictures licensed under the Creative Commons Attribution 2.0 Generic. Attribution: Damo 1977, and Robert Clarke, respectively. Danny Dyer, Jean Dujardin, and Tom Mison: Pictures licensed under the Creative Commons Attribution: Hilton1949, Georges Biard, and Floatjon, respectively. Nicholas Hoult: Pictures licensed under the Creative Commons Attribution-Shared Alike 2.0 Generic. Attribution: Gage Skidmore. Jack O'Connell: Pictures licensed under the Creative Commons Attribution-Shared Alike 2.0 Generic. Attribution: gdcgraphics.

of these faces (i.e., physical distinctiveness as compared to unfamiliar faces; differences between famous face identities in within-person variability), or else to a combination of both factors.

Resolving these issues is critical, not only to better characterize and understand differences between familiar and unfamiliar faces in the human brain, an important and debated topic in human face recognition research (Rossion, 2018; Young & Burton, 2018), but also because this EEG measure could prove extremely useful to implicitly and rapidly measure someone's degree of familiarity with a given face identity. To do so, the present study extends the measure of the EEG frequency-tagged facial identity recognition neural response (Zimmermann et al., 2019) to two groups of participants tested exactly in the same conditions, but differing only with respect to their long-term familiarity with the face celebrity appearing periodically among unfamiliar faces. The faces of two different French celebrities (actors Dany Boon and Jean Dujardin) giving rise to variable response amplitudes in the original study are tested here with six unfamiliar celebrities in a fully controlled paradigm (i. e., with the same number of repetitions for each familiar or unfamiliar face identity). Given that (familiar) face identity recognition in humans is largely impaired following picture-plane inversion (Yin, 1969; Collishaw & Hole, 2000; Busigny & Rossion, 2010; Besson et al., 2017), stimulation sequences with upright faces are compared to the same sequences with faces appearing upside-down, allowing to further isolate high-level neural recognition effects. Under the hypothesis that the frequencytagged neural familiar face identity response is essentially due to a long-term familiarity effect, we predicted significantly reduced recognition responses over the occipitotemporal regions in the unfamiliar, compared to the familiar participant group tested with the exact same conditions, and quantified this familiarity effect at both the group and individual participant level.

Methods

Participants

We initially recruited 34 participants in the experiment (17 who were familiar with the two celebrities used, i.e., the familiar group, and another 17 who were unfamiliar with these two faces, i.e., the unfamiliar group). They were given a familiarity questionnaire (Names Questionnaire) before and another questionnaire (Faces Questionnaire) after their EEG testing (adapted from Zimmermann et al., 2019). The Names Questionnaire included the written names of 8 face identities presented in the experiment. Only two identities, French actors D. Boon and J. Dujardin were selected for their high degree of familiarity among the young Frenchspeaking adult population of Belgium, where the experiment was carried out. Participants were required to indicate ('yes or no') whether they knew these famous identities by their name, and whether they could mentally visualize their face. In the Faces Questionnaire, participants were shown an exemplar (randomly selected from the testing stimulus set) of each of the 8 face identities and they had to write down the name and

profession of all the face identities that they could recognize.

For the familiar group, data of one participant was excluded due to excessive noise/muscular artifact during EEG recording, and another two because they did not recognize one of the two familiar face identities used in the experiment. All the remaining 14 participants (9 females, mean age = 22.6 ± 2.1 years old, range = 20-25 years old, all right handed) reported knowing the two familiar face identities very well (i.e., reported to know the faces, to have seen the identities very often on social media, and also to be able to recall their name and profession). For the unfamiliar group, all 17 participants were short-term (i.e., 3 to 6 months) exchange Caucasian students who were non-French speakers. Data of two participants were excluded from further analysis because they reported to be highly familiar to one of the two French celebrities. Another participant was excluded because her data was not saved successfully due to technical issues. The final sample consisted of 14 participants (7 females, mean age = 25.65 ± 4 years old, range = 20-32 years old, all right handed) who were not familiar with (i.e., did not know) the two French celebrities. The participants in the unfamiliar group were slightly older than those in the familiar group, $t_{(26)} =$ 2.55, p < 0.5, but this difference played no role in the results observed (see supplemental material).

The final sample size in each group meets the criteria (total sample size = 13) based on a power analysis of a recent study by Zimmermann et al. (2019) (paired t-test on difference between upright and inverted face conditions, $d_z = 1.13$, power = 0.95). The power analysis was calculated with G*power (Faul, Erdfelder, Lang, & Buchner, 2007).

All participants were paid 10 euros per hour as compensation upon completion of the study. They had normal or corrected-to-normal vision and no prior history of neurological illness. In accordance with the University of Louvain Biomedical Ethics Committee guidelines (ref. no. B403201111965), participants gave written informed consent prior to testing. None of the tested participants reported impairments in individual face recognition, which was also assessed with an electronic version of the Benton Facial Recognition Test (BFRT-c) (Benton et al., 1983 for the original test; electronic version in Rossion & Michel, 2018). There was no difference in performance at the BFRT-c - a face matching test with pictures of unfamiliar faces - between two groups of participants, $t_{(26)} = 0.45$, p > .1 (Familiar, $M = 83.7 \pm 6.8\%$, on average 45.21 items correct out of 54; Unfamiliar, M = $84.8 \pm 5.6\%$, in average 45.79 items correct out of 54). Their overall performance was in the range of the average score in a similar population of participants (≈ 83%) (Rossion & Michel, 2018).

Stimuli

Stimuli consist of 160 color images of male famous celebrity faces (eight different face identities of which two were the familiar targets, see Figure 1 for examples). The two French celebrities D. Boon and J. Dujardin (same images as used in the Zimmermann et al., 2019 study) served as the familiar faces appearing periodically, in different sequences. In the previous study, these two celebrities both gave rise to robust but variable amplitude of the neural familiar face identity response, with a larger response to D. Boon than J. Dujardin (Zimmermann et al., 2019). They were selected here both to investigate whether the same response patterns would be replicated in the current study with another group of participants familiar with these two identities, and to test the extent to which the variability of the familiar face identity response depends on familiarity. Six randomly chosen faces (out of 15 from Zimmermann et al., 2019 study) of moderately famous British people served as unfamiliar faces in the experiment. For each face identity, we selected a highly variable set of 20 different images, with faces varying substantially in background context, size, head orientation, lighting conditions, expression, etc. The average image for each face identity and the variances of images are shown in Figure 2. Images were 255 pixels in height, while their width varied (187 \pm 13 pixels) to preserve the variations in head width of different identities. The ratio between head width and image width of familiar identities did not differ from those of unfamiliar faces (ps > 0.1, Bonferroni corrected). All face stimuli were presented at upright orientation in half of the sequences and at inverted orientation in the remaining half of the sequences. The order of the orientation conditions was randomized across participants.

Procedure

EEG testing was performed during only four different stimulation sequences (2 with upright face images and 2 with inverted faces) of 70 s stimulation each. The four stimulation sequences were repeated once, resulting in eight stimulation sequences in total (about 10 min of testing). They were presented in randomized order for each participant. Different images of unfamiliar faces were presented at a predefined frequency of 6 Hz (166 ms stimulus onset asynchrony, SOA), allowing only one gaze fixation to each face. In each sequence, widely variable images of the same identity, either D. Boon or J. Dujardin (in different sequences), were embedded every 7 images (replacing an unfamiliar image), providing a second presentation rate of 6/7 Hz (i.e., 0.86 Hz) (Figure 1). All other face identities appeared randomly.

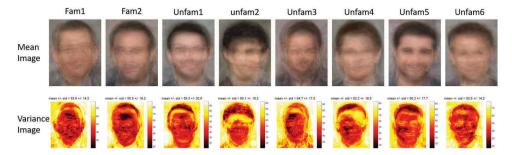


Figure 2. Mean (upper panel) and variance (lower panel) images of each face identity used in the experiment (Fam1: D. Boon; Fam2: J. Dujardin). Each image was calculated based on the 20 natural images of a particular identity. Darker colors in the variance images, compared to light colors, indicate areas of the faces where there are less variability across images.

Since we used six unfamiliar faces with 20 images each, both the number of exemplars of each face identity (for both familiar and unfamiliar faces) and the presentation times (i.e., 3 times) of each image were fully balanced, an additional methodological control as compared to the previous study (Zimmermann et al., 2019).

Following the principle of EEG frequency-tagging (Adrian & Matthews, 1934; Regan, 1966; Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015 for review), an image presentation rate of 6 Hz should elicit a robust EEG response at exactly 6 Hz and its harmonics (12 Hz, 18 Hz, etc.), reflecting a general visual stimulation response to all face stimuli. Most importantly, the periodically repeated face identity (i.e., D. Boon or J. Dujardin) should elicit a significant face identity recognition response at 0.86 Hz and harmonics (1.71 Hz, 2.57 Hz, etc.) for participants in the familiar group, providing that it elicits a periodically repeated (i.e., generalized) differential response to the other unfamiliar face identities (see, e. g.,, Liu-Shuang, Norcia, & Rossion, 2014; Lochy, Van Belle, & Rossion, 2015; Rossion, Jacques, Torfs, & Liu-Shuang, 2015; for the principles of this approach, and applications to measure various visual recognition functions).

During the whole testing session, participants were required to monitor a central fixation cross that appeared in the middle of the images throughout each stimulation sequence, while simultaneously paying attention to the flickering stimuli. They had to press the SPACE bar of a keyboard whenever they saw the color change of the fixation cross (from black to red, 200 ms duration, 15 change occurrences in each sequence at random times), as accurately and as rapidly as possible. Thus, there was no explicit face-related task during the experiment.

EEG recording

One hundred and twenty-eight-channel (Ag-AgCl Active-electrodes) EEG was recorded (Biosemi Active 2

system, BioSemi, Amsterdam, the Netherlands) with a sample rate of 512 Hz. Recording sites included standard 10–20 system locations as well as additional intermediate positions (http://www.biosemi.com/headcap.htm, relabeled to more conventional labels of the 10–5 system, see Supplemental Fig. S1 in Rossion et al., 2015). The magnitude of the offset of all electrodes, referenced to the common mode sense (CMS), was held below 50 mV. Vertical and horizontal electrooculogram (EOG) was recorded using four extra flat-type Active-electrodes: two above and below participant's right orbit, and two lateral to the external canthi of the two eyes.

Analysis

Preprocessing

Analysis of the recorded EEG was preformed using Letswave 5 (https://github.com/NOCIONS/Letswave5), running on MATLAB R2013a (MathWorks, USA). The preprocessing steps were largely identical to previous studies with this frequency-tagging approach (e.g., Quek, Nemrodov, Rossion, & Liu-Shuang, 2018; Retter & Rossion, 2016; Zimmermann et al., 2019). For each participant, the raw EEG signal was band-pass filtered between 0.1 Hz and 100 Hz (24 dB/Octave). The electrical noise at 50 Hz and two following harmonics (100 Hz and 150 Hz) was notch-filtered with a width of 0.5 Hz. EEG data were segmented including 2 s before and after each 74 s (including 2 s fade-in and 2 s fade-out) sequence. Artifact-prone channels with deflections larger than 100 μV across multiple sequences (less than 0.5% of channels on average) were interpolated. Eyeblink artifacts were corrected by applying independent component analysis (ICA) on the data of 4 participants (1 participant in the infamiliar group and 3 participants in the unfamiliar group) who blinked more than 0.2 times/s on average during the sequences (Retter & Rossion, 2016). All channels were then referenced to a common average.

Frequency domain analysis

EEG recordings were re-segmented to contain an integer number of familiar face presentation cycles (Retter & Rossion, 2016). For each individual, we collapsed sequences in the time domain across the two familiar celebrities for each face orientation condition. A Fast Fourier Transform (FFT) was then applied to represent the data as a normalized amplitude spectrum (uV) for each channel. Each spectrum had a high resolution of approximate 0.014 Hz (1/70s), which allowed the unambiguous identification of the face identity recognition response at the presentation rate of 0.86 Hz (and harmonics, e.g., 1.71 Hz, etc.). Similarly, the FFT was also applied separately to each individual familiar face identity (averaged across two sequences with the same identity presented), for each orientation condition, respectively.

Baseline EEG activity was estimated as in previous studies (e.g., Liu-Shuang et al., 2014, 2016; Retter & Rossion, 2016; Zimmermann et al., 2019), with the neighboring 20 bins surrounding the frequency bins of interest (10 bins by each side, excluding the immediately adjacent bins in case of remaining spectral leakage, and the local maximum and minimum amplitude bins to avoid projecting the signal in the noise EEG spectrum). Then, baseline correction of the EEG responses was applied with two methods: (1) division by the EEG noise to show EEG spectrum in signal-to-noise ratio (SNR), allowing to better visualize small responses and (2) Subtraction of the EEG noise (baseline subtraction, SBL) to quantify responses in μV across harmonics.

For the two presentation frequencies (6 Hz and 0.86 Hz), there were responses reflected at multiple harmonics (Figures 3 and 4), in line with previous studies (e.g., Liu-Shuang et al., 2014; Retter & Rossion, 2016; Zimmermann et al., 2019). From visual inspection, the harmonic response patterns and scalp topographies for both the base rate response (6 Hz) and the face identity recognition response (0.86 Hz) were consistent with those of our recent study, with responses above noise up to the 9th harmonic (7.71 Hz, Zimmermann et al., 2019). Therefore, in the main analysis, we quantified the face identity recognition response by summing the baseline-corrected amplitudes of all eight harmonics, excluding the base rate. The general visual response was quantified as the sum of the first nine significant harmonics (6 Hz, 12 Hz, etc.).

In a complementary analysis (supplemental material), we selected the significant harmonics according to the grand-averaged response patterns across all participants in both groups (i.e., familiar and unfamiliar) and across all channels and both face orientation conditions (Retter & Rossion, 2016; Zimmermann et al., 2019). We computed a z-score at each discrete frequency bin with the formula z = (x-baseline mean)/(baseline standard deviation), withthe same baseline response quantification as mentioned above. We used a z-score threshold at 1.64 (p < .05, onetailed, i.e., signal > noise) to select significant harmonics (Retter & Rossion, 2016; Zimmermann et al., 2019). In this way, six significant harmonics (i.e., 1.71 Hz, 2.57 Hz, 3.43 Hz, 4.29 Hz, 5.14 Hz, and 7.71 Hz) were identified, and summed to quantify the face identity recognition response. We used the same approach to quantify the general visual responses at 6 Hz, by summing the baseline-corrected amplitudes of the first nine significant harmonics (i.e., 6 Hz, 12 Hz, and up to 54 Hz).

We statistically tested neural responses at two levels: across the whole scalp channels and at local regions-ofinterest (ROIs) where the two responses at 0.86 Hz and 6 Hz (and their harmonics) reached to maxima, consistent with previous studies with the same FPVS-EEG paradigm measuring individual unfamiliar face discrimination responses (Dzhelyova & Rossion, 2014a, 2014b; Liu-Shuang et al., 2014; Xu, Liu-Shuang, Rossion, & Tanaka, 2017). Therefore, a middle occipital ROI was defined (average across 12 middle posterior channels POO5&6, POOz, O1&2, Oz, POI1&2, Olz, I1&2, and Iz), and a bilateral occipitotemporal ROI (OT ROI; average across 10 posterior channels P7&8, P9&10, PO7&8, PO9&10, PO11&12). As in previous studies, the OT ROI was further split it into two ROIs, left OT ROI (channels over the left hemisphere, P7, P9, PO7, PO9, PO11), and right OT ROI (channels over the right hemisphere, P8, P10, PO8, PO10, PO12), to examine potential hemispheric differences in familiar face identity recognition.

We further quantified each participant's individual face identity recognition response over the OT ROI, by calculating a z-score based on the summed-harmonic response amplitudes at 0.86 Hz and its 20 neighboring bins (the same formula as mentioned above). A significant recognition response was noted with a threshold at a z-score of 1.64 (p < .05, one-tailed).

To examine the response differences between two participants groups in different face orientation conditions, we ran mixed-ANOVAs on the baseline-corrected amplitudes. Greenhouse-Geisser correction for degrees of freedom was applied whenever sphericity was violated. For significant effects, post-hoc t-tests were conducted to examine differences between conditions with Bonferroni correction. To test whether variability in response amplitude across face identities is related to familiarity or other factors, we also separately examined the recognition response of each periodically presented familiar face identity (D. Boon and J. Dujardin) for each group.

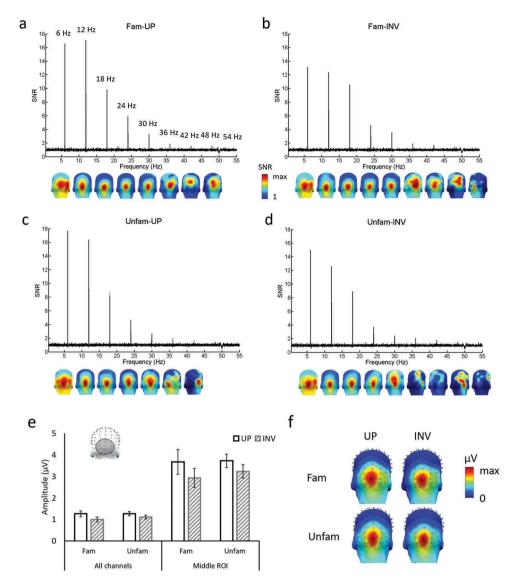


Figure 3. Grand-averaged general visual presentation responses. Grand-averaged EEG spectra in SNR, at 6 Hz and subsequent harmonics (12 Hz, 18 Hz, and so forth), over the middle occipital ROI (averaged across channels POO5&6, POOz, O1&2, Oz, POI1&2, Olz, I1&2, and Iz) are shown for both face conditions in the familiar group (ab) and unfamiliar group (cd). Three-D scalp maps are shown below for each significant harmonic. The color scale indicates the range from 1 to the maximum SNR of each harmonic response. e. Grand-averaged responses in baseline-corrected amplitudes (μV) between familiar and unfamiliar groups in both upright (UP) and inverted (INV) face conditions over all scalp channels and middle occipital ROI. Error bars indicate standard error of the mean. f. Three-D scalp topographies of summed-harmonic general visual responses shown separately for upright and inverted faces for both groups. Color scale indicates the range from 0 to the maximum amplitude of each condition.

Results

Behavioral results (fixation cross task)

We computed mean accuracy and response times (RTs) to fixation cross color changes for each participant. RTs were calculated according to the onset of target fixation cross. Responses were considered as correct if they occurred between 150 and 1000 ms following target onset. Accuracy for the fixation task was very high across conditions. A mixed-ANOVA on accuracy with *Group* (familiar, unfamiliar) as between-subjects factor and *Orientation*

(upright, inverted) as within-subjects factor showed that there was no difference between groups (F(1,26) = 0.27, p > .1, $\eta^2 = 0.01$; Familiar, $M = 98.7 \pm 2.4\%$; Unfamiliar, $M = 98.2 \pm 2.4\%$), or between different face orientations (F(1,26) = 1.79, p > .1, $\eta^2 = 0.07$; Upright, $M = 98 \pm 3.6\%$; Inverted, $M = 98.9 \pm 2\%$). However, a similar mixed-ANOVA on RTs showed that responses were slightly (6 ms) slower in the upright face condition, compared to the inverted condition, reflected by a significant main effect of *Orientation* (F(1,26) = 4.26, p = .05, $\eta^2 = 0.14$; Upright, $M = 452 \pm 46$ ms; Inverted, $M = 446 \pm 44$ ms). There was no difference in RTs between

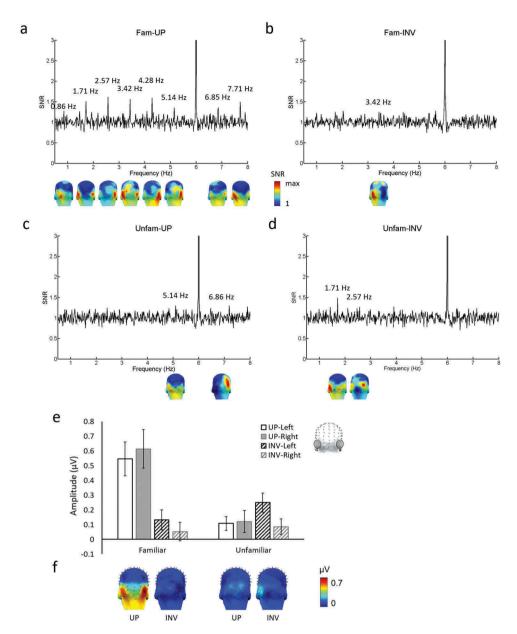


Figure 4. Face identity recognition responses in SNR at 0.86 Hz (and harmonics) at OT ROI (average across P7&8, P9&10, PO7&8, PO9&10, PO11&12), shown separately for the familiar (Fam) group in upright (UP) and inverted (INV) face conditions (a and b), and the unfamiliar (Unfam) group in both face orientation conditions (c and d). Three-D scalp topographies show significant responses with color scale indicating the range from 1 to the maximum SNR of each condition. e. Grand-averaged face identity recognition responses in baseline-corrected amplitudes (µV) of both groups as a function of face orientation over bilateral OT ROI. Error bars indicate standard error of the mean. f. Three-D scalp topographies of summed-harmonic individual face recognition response shown for each condition.

groups (F(1,26) = 0.01, p > .1, $\eta^2 = 0.00$; Familiar, $M = 450 \pm$ 45 ms; Unfamiliar, $M = 448 \pm 45$ ms).

EEG results

Frequency domain indexes of general visual responses

The base stimulation rate of 6 Hz elicited significant (p < 1.05) responses at the first nine consecutive harmonics (i. e., 6 Hz, 12 Hz, and so forth). This was found across participant groups and across face orientation conditions (Figure 3). Consistently, the first harmonic at 6 Hz was associated with activations over the occipitotemporal region in addition to the middle occipital focus across conditions (Zimmermann et al., 2019; see supplemental material for separate analysis with the first harmonic at 6 Hz and the sum of remaining harmonics). Harmonic responses decreased significantly beyond the first 3 harmonics (i.e., 6 Hz, 12 Hz, and 18 Hz; Figure 3).

A mixed-ANOVA with Orientation (upright, inverted) as within-subjects factor and Group (familiar, unfamiliar) as between-subjects factor on the responses averaged across all scalp channels showed that there was a significant main effect of Orientation, F(1,26) = 14.49, p < .001, $n^2 = 0.36$ (Upright, $M = 1.27 \pm 0.44 \mu V$; Inverted, $M = 1.05 \pm 0.044 \mu V$; Inverted, $M = 1.044 \mu V$; Inverted, 0.36 μ V). Neither the main effect of *Group*, F(1,26) = 0.14, p > .1, $n^2 = 0.01$, or its interaction with *Orientation*, F(1,26)= 0.93, p > .1, $\eta^2 = 0.04$, was significant. The same response pattern was replicated over the middle occipital ROI. Visual responses were larger for upright compared to inverted images (Upright, $M = 3.70 \pm 1.80 \mu V$; Inverted, $M = 3.08 \pm 1.41 \mu V$), reflected by a significant main effect of *Orientation*, F(1,26) = 14.91, p < .001, $\eta^2 = 0.36$. The main effect of *Group*, F(1,26) = 0.09, p > .1, $\eta^2 = 0.00$, and the interaction of Orientation \times Group, F(1,26) = 0.59, p > .1, $\eta^2 = 0.02$, were not significant (Figure 3).

Frequency domain indexes of face identity recognition response

There were major differences in the face identity recognition responses across groups (Figure 4). Over bilateral OT regions, we observed high SNR responses at the familiar face identity stimulation frequency of 0.86 Hz and its harmonics (e.g., 1.71 Hz, 2.57 Hz, and so forth, skipping the 6 Hz base frequency) at the upright face condition for the familiar group. The responses reduced strongly when all face images were inverted, with only the fourth harmonic (i.e., 3.42 Hz) achieving significance. For the unfamiliar group of participants, tested with the exact same sequences, the responses were barely visible, with only two significant harmonics (i.e., 5.14 Hz, and 6.85 Hz) for the upright images, and another two significant (e.g., 1.71 Hz, and 2.57 Hz) for the inverted images.

In the main analysis, the face identity recognition response was quantified as the sum of the first eight harmonics at 0.86 Hz, in both groups. Note that even if most harmonics are not significant on grand average data for the group of participants unfamiliar with the two French celebrities, the correct procedure to compare the two conditions is to sum the amplitude values of the same baseline-corrected harmonics (separately) for the two conditions in order to quantify the respective response (i.e., if the signal is not above noise level for some harmonics in the unfamiliar group, this amounts to adding zeros to the summed response). Note that although the quantified response was much larger for the familiar group tested with upright faces, both upright face conditions (familiar and unfamiliar groups) were associated with significant responses above zero (both ps < .05, one-tailed).

When considering face identity recognition responses across all scalp channels, a mixed ANOVA with Orientation (upright, inverted) as within-subjects factor and Group (familiar, unfamiliar) as between-subjects factor showed no significant main effect of Orientation and no Orientation \times Group interaction (both ps > .1). The main effect of Group reached to a marginal significance, F(1,26) = 3.52, p = .07, $n^2 = 0.12$, reflecting a borderline larger recognition response in the familiar group (Familiar, $M = 0.11 \pm 0.07 \mu V$; Unfamiliar, $M = 0.06 \pm 0.06 \mu V$) 0.07 µV). A similar mixed ANOVA was also run over the middle occipital ROI. We found a main effect of Orientation, F(1,26) = 4.59, p < .05, $\eta^2 = 0.15$, reflected by a larger response to upright faces than inverted faces (Upright, $M = 0.25 \pm 0.24 \,\mu\text{V}$; Inverted, $M = 0.11 \pm 0.23$ μ V). No other effect was significant (both ps > .1).

Over the OT ROI, where the face identity recognition response was maximal, we ran a mixed ANOVA with Orientation (upright, inverted), and Hemisphere (left, right) as within-subjects factor and Group (familiar, unfamiliar) as between-subjects factor. The results showed a significant main effect of Orientation, F(1,26) = 9.55, p <.01, $\eta^2 = 0.27$ (Upright, $M = 0.35 \pm 0.39 \,\mu\text{V}$; Inverted, M = $0.13 \pm 0.18 \mu V$). In this ROI, the main effect of *Group* was also significant, F(1,26) = 8.25, p < .01, $\eta^2 = 0.24$, due to larger responses for the familiar group than the unfamiliar group (Familiar, $M = 0.34 \pm 0.24 \,\mu\text{V}$; Unfamiliar, $M = 0.14 \pm$ 0.1 µV). These effects were however modulated by a significant interaction Orientation \times Group, F(1,26) =14.78, p < .001, $\eta^2 = 0.36$. Further analyses showed that there was only an inversion effect for the familiar group, $t_{(13)} = 4.14$, p < .001 (Upright, $M = 0.58 \pm 0.41$ µV; Inverted, $M = 0.09 \pm 0.2 \,\mu\text{V}$; unfamiliar group: $t_{(13)} = 0.69, p > .1$, Upright, $M = 0.11 \pm 0.19 \,\mu\text{V}$; Inverted, $M = 0.17 \pm 0.15 \,\mu\text{V}$). Another decomposition of the interaction showed that the response at upright orientation was much larger in the familiar than the unfamiliar group, $t_{(26)} = 3.86$, p < .001, while there was no difference between groups at inverted orientation, $t_{(26)} = 1.11$, p > .1. There was no main effect of Hemisphere, F(1,26) = 0.83, p > .1, $\eta^2 = 0.03$, or any other effect (all ps > .1).

The results were strictly identical when considering only the first six significant harmonics (harmonics 2–6 and 9), based on averaged amplitude spectra across groups and face orientation conditions (see supplemental material).

Face identity recognition responses for each familiar face identity

To examine whether different familiar face identities showed different response patterns, we ran another

mixed-ANOVA over the OT ROI with Identity (D. Boon, J. Dujardin), and Orientation (upright, inverted), and Hemisphere (left, right) as within-subjects factors, and Group (familiar, unfamiliar) as between-subjects factor (Figure 5). As in the analysis above, there were significant main effects of *Orientation*, F(1,26) = 12.5, p < .01, $n^2 = 0.33$, showing larger responses to the upright than inverted faces (Upright, $M = 0.36 \pm 0.05 \mu V$; Inverted, $M = 0.15 \pm$ 0.03 μ V) and Group, F(1,26) = 6.22, p < .05, $\eta^2 = 0.19$, with a familiar group advantage (Familiar, $M = 0.33 \pm 0.04 \mu V$; Unfamiliar, $M = 0.18 \pm 0.04 \,\mu\text{V}$), and their interaction, F(1,26)= 18.21, p < .001, $\eta^2 = 0.41$, showing significant face inversion effect, $t_{(13)} = 4.68$, p < .001, for the familiar group (Upright, $M = 0.56 \pm 0.34 \,\mu\text{V}$; Inverted, $M = 0.1 \pm 0.18 \,\mu\text{V}$) and not for the unfamiliar group (Upright, $M = 0.16 \pm 0.16$ μ V; Inverted, $M = 0.2 \pm 0.15 \mu$ V). Importantly with respect to the goals of the study, there was a main effect of *Identity*, F(1,26) = 8.77, p < .01, $\eta^2 = 0.25$, with the face identity recognition response to *D. Boon* being larger than to J. Dujardin (D. Boon, $M = 0.37 \pm 0.05 \mu V$; J. Dujardin, $M = 0.15 \pm 0.04 \mu V$). However, there was no significant interaction between *Identity* and other factors (all ps > .1). The other comparisons were not significant (all ps > .1).

Robust neural indexes of face identity recognition response in each individual participant

The majority of participants in the familiar group showed significant responses over either unilateral or bilateral OT ROI (Figure 6). We quantified these responses by calculating the z-score (with a threshold of z-score > 1.64, p < .05; see Methods section) for each participant separately for upright and inverted images (averaged across familiar face identities). In the familiar group, 13 out of 14 participants (except #P8) showed significant neural face identity recognition responses over OT ROI on upright images (zscore range 1.7-8.5). For inverted images, only two participants (#P6 and #P13) showed a significant response (range 1.8-4.7). Twelve (except #P8 and #P13) out of 14 participants showed a significant inversion effect (range 1.7–10.5). In contrast, for the unfamiliar group, five out of 14 participants showed significant responses for upright faces (range 2.1-3.5), and eight out of 14 participants showed significant responses for the inverted faces (range 1.7-6.6). Only three out of 14 participants showed a significant inversion effect (range 2-3.6).

Discussion

We replicated the large frequency-tagged facial identity recognition neural response elicited in people who -were familiar with a periodically repeated celebrity face appearing among unfamiliar faces (Zimmermann et al., 2019). This response is elicited automatically (i.e., without intention/ instruction to do so) to natural images of faces presented under severe time-constraints. The novel finding of the present study is that the response is also found in participants who do not know the periodically repeated celebrity, but it is reduced by about a factor of five for upright images (i.e., 0.58 µV for familiar participants vs. 0.11 µV for unfamiliar participants). Given that different facial identities can give rise to substantially different electrophysiological responses in this paradigm (Zimmermann et al., 2019), this between-groups comparison was preferred here rather than comparing the periodic repetition of a familiar vs. an unfamiliar face identity in the same group of participants. The large amplitude difference of the EEG response observed here cannot be due to general differences between the groups of participants, who were matched in terms of gender and ethnicity and with a small age difference such that these factors played no role in the results (supplemental material). Moreover, the two groups

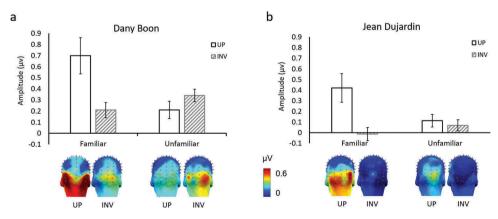


Figure 5. Grand-averaged face identity recognition responses in baseline-corrected amplitudes (μV) of both groups as a function of face orientation over bilateral OT ROI, for a. D. Boon and b. J. Dujardin. Error bars indicate standard error of the mean. Three-D scalp topographies of summed-harmonic individual face recognition response shown for each condition.

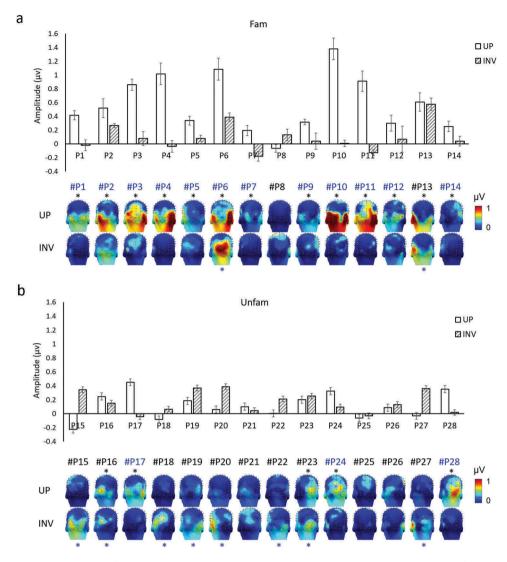


Figure 6. Grand-averaged individual face recognition response in baseline-corrected amplitude (μ V) shown for each participant in a. the familiar group and b. the unfamiliar group as a function of face orientation. Topographical scalp maps of summed-harmonics at OT ROI for upright (UP) versus inverted (INV) sequences, shown separately for individual participants in both groups (familiar and unfamiliar). Scalp topographies with a black asterisk show a significant z-score for upright sequences, and a blue asterisk for inverted sequences. Participants with a significant face inversion effect are shown with blue labels.

did not differ in their behavioral performance at the orthogonal task, in terms of the basic EEG response to all visual stimuli (i.e., 6 Hz and harmonics), and in the amplitude of their face identity recognition neural response when the images were presented upside-down.

The frequency-tagging paradigm allows an objective identification and a relatively straightforward quantification of the neural facial identity recognition response in the EEG frequency-domain, revealing that the response for participants unfamiliar with the faces is of about 20% of amplitude as compared to the response obtained in participants familiar with the faces. This observation indicates that the bulk of the neural response is not due to shared repeated physical features of the periodically

presented face identity independently of long-term memory, but rather to people's long-term memory representation of that face identity in the occipitotemporal cortex. This response therefore essentially reflects a *cortical memory effect* and can index people's familiarity with a given face identity.

In humans, substantial behavioral differences have been found between familiar and unfamiliar faces, especially in terms of the ability to associate different views of the same face identity: people are generally much better with pictures of familiar than unfamiliar faces (e.g., Bruce, 1982; Jenkins et al., 2011; White, Kemp, Jenkins, Matheson, & Burton, 2014; see Young & Burton, 2018). Yet, despite these differences, it is fair to say that

previous EEG studies have reported rather modest and inconsistent neural differences between pictures of familiar and unfamiliar faces (Alsufyani et al., 2018; Andrews, Burton, Schweinberger, & Wiese, 2017; Barragan-Jason, Cauchoix, & Barbeau, 2015; Barrett, Rugg, & Perrett, 1988; Caharel, Courtay, Bernard, Lalonde, & Rebaï, 2005; Collins, Robinson, & Behrmann, 2018; Gilad-Gutnick, Harmatz, Tsourides, Yovel, & Sinha, 2018; Huang et al., 2017; Jemel, Schuller, & Goffaux, 2010; Kloth et al., 2006; Lui, Lui, Wong, & Rosenfeld, 2018; Wiese et al., 2019; Zimmermann & Eimer, 2013), at least in implicit tasks (e.g., unlike in Barragan-Jason et al., 2015; Caharel, Ramon, & Rossion, 2014). This is also the case in functional magnetic resonance imaging studies (Natu & O'Toole, 2011 for review; e.g., Ramon, Vizioli, Liu-Shuang, & Rossion, 2015). A potential factor contributing to the lack of substantial consistent familiarity effects could be the lack of reliance on ecologically valid natural images in most studies, as suggested by the recent report of a clear difference in brain potentials elicited by variable natural images of personally familiar versus unfamiliar faces (Wiese et al., 2019). However, in that latter study, the difference between faces of celebrities and unfamiliar faces - as tested here - was relatively small and detected significantly in only 5 of 18 participants. Yet, impressively, in the present study, 13 out of 14 participants who knew the two celebrities faces showed a significant neural facial identity recognition response, this response being significantly larger for upright than inverted faces in 12 participants. Moreover, these results were obtained with only four stimulation sequences at upright orientation, for a total of about only 5 min of testing by participant. Considering the findings of Wiese et al. (2019), this suggests that the present paradigm would even be more sensitive with pictures of personally familiar faces, which are generally associated with the most robust representations (Ramon & Gobbini, 2018).

As discussed previously (Zimmermann et al., 2019), the high sensitivity of the present approach could be attributed to several factors such as the high number of images of celebrities inserted in each sequence at this fast stimulation rate (i.e., 240 presentations of the two celebrities) and the high-frequency resolution of the approach, so that there is little EEG noise in the smallfrequency bins capturing all of the signals (Regan, 1989; Rossion, 2014). Most importantly, previous EEG studies compare responses to the sudden appearance of a familiar vs. an unfamiliar face identity against a uniform visual field, these responses being largely dominated by nonspecific visual processes. In contrast, in a frequency-tagging approach, the visual system is continuously stimulated, the general common neural response to the familiar and unfamiliar faces is confined to the 6 Hz response and its harmonics (12 Hz, etc.), constituting a baseline signal. Therefore, all of the 0.86 Hz response is a differential neural response that emerges only if a population of neurons respond specifically (or differently) to the periodically repeated familiar face identity (see, e.g., Retter & Rossion, 2016; Rossion et al., 2015 for a similar logic in measuring selective responses to natural images of faces as a category; Lochy et al., 2015 for differential responses between words and pseudowords).

Here, as also found previously, there was a large reduction of the facial identity recognition neural response for familiar faces with upside-down inversion of the facial stimuli, also by about a six-fold factor. This reduction with inversion is in line with the drop of performance observed in behavioral tasks measuring the identity recognition of familiar faces (e.g., Besson et al., 2017; Busigny & Rossion, 2010; Collishaw & Hole, 2000). While the inversion effect is also consistently found in behavioral studies requiring to match pictures of unfamiliar faces (e.g., Freire, Lee, & Symons, 2000; Yin, 1969; see Rossion, 2008 for review), inversion did not further reduce the weak EEG response obtained here in the group of participants who were unfamiliar with the periodically repeated celebrity. This could be due to a floor effect for the periodically repeated face identity in the unfamiliar group. Alternatively, it could be that the weak repeated distinction between a repeated unfamiliar identity and other unfamiliar identities is not based on a high-level facial configuration but on local features preserved by inversion.

Importantly, we consider that the weak effect response found here in the unfamiliar group should not be interpreted as evidence that neurotypical adults are 'poor' at matching variable images of unfamiliar faces (e.g., Megreya & Burton, 2006; Jenkins et al., 2011; White et al., 2014; see Rossion, 2018 for a brief discussion of this issue). Rather, this could be attributed to the extremely challenging stimulation condition of the paradigm: the variable images of the periodically repeating unfamiliar face identity are not presented side-by-side, they appear only briefly, with many interleaved pictures of other unfamiliar face identities. Most critically, for the group of participants who do not know the celebrity, the periodically repeated unfamiliar face identity appears among, i.e., against, other unfamiliar faces in this paradigm. If the base faces were all familiar faces, a larger response for a periodically repeated unfamiliar face identity and a more modest response for the familiar face would be expected.

The neural face identity recognition response effect was significantly larger for one of the celebrities, D. Boon, than the other, J. Dujardin, consistent with the response

patterns found in Zimmermann et al.'s (2019) study. However, interestingly, the difference between the two identities also holds for the group of participants who do not know these faces, a novel finding of the present study. This suggests that the difference in magnitude of the neural response across the two familiar face identities is not due to their degree of familiarity per se. Rather, factors such as face distinctiveness (in general, e.g., Valentine & Bruce, 1986, and as compared to the unfamiliar faces used in the experiment) and withinperson variability (in real life, e.g., Jenkins et al., 2011, and in the specific image set selected in the experiment), may be critical in accounting for variability in the EEG amplitude of the face identity recognition response. Here, and in the previous study, within-person variability and face distinctiveness, which are difficult to quantify on variable natural images, might be both higher for D. Boon than J. Dujardin (Figure 2). Therefore, including inverted faces to control for image distinctiveness and within-person (image) variability of some images may be important to optimize the current paradigm.

Although there was a substantial amount of interindividual variability in the scalp localization of the peak of activity for the neural face identity recognition response, the effect was consistently observed over bilateral occipitotemporal electrodes. The lack of right hemispheric lateralization - which is typical of unfamiliar face individuation in such frequency-tagging paradigms (e.g., Liu-Shuang et al., 2014) - could be precisely because unfamiliar faces preferentially recruit the right hemisphere at the group level, as also indicated by the 6 Hz response (Figure 4). Hence, the neural face identity recognition response expressed in contrast to unfamiliar faces is no longer right lateralized. Another potential factor is that the neural response recorded here may also reflect automatic triggering of semantic information and a famous name associated with the rapidly repeated famous identity, with the left hemisphere playing a more important role than the right hemisphere in these processes (e.g., Gainotti, 2013; Rice, Caswell, Moore, Lambon Ralph, & Hoffman, 2018). The limited spatial resolution of EEG does not allow us to provide more specific information about the sources of the effect recorded on the scalp. However, the memory effect is likely to reflect the strengthening of visual representations in the visual occipitotemporal cortex, including in the anterior temporal lobe, rather than the direct contribution of structures of the medial temporal lobe such as the hippocampus, which may rather be essential to learn, consolidate and explicitly recall these visual representations in the visual cortex (Squire, Genzel, Wixted, & Morris, 2015; Sekeres, Winocur, & Moscovitch, 2018 for reviews). Testing this paradigm with intracerebral human recordings (e.g., Jonas et al., 2016) in future studies should provide a clearer answer regarding the source of the neural face identity recognition response.

Finally, the present neural face identity recognition response may prove to be an important measure not only due to the high sensitivity and objectivity of the approach but also because it is implicit, i.e., recorded while participants are not asked to recognize the repeated face identity. Hence, the approach could be used to determine whether someone is familiar with a given face identity even if the specific images have not been seen before and without requiring an explicit response. To be more accurate, such an evaluation should include the use of a condition with inverted images, which allows isolating the effect of long-term face familiarity from the effect of physical distinctiveness or within-face identity physical variability, and could be standardized in participants who are not familiar with the periodically repeated face identity. In these conditions, the paradigm as used here could prove invaluable for further understanding of the nature of human familiar face identity recognition (i.e., its sensitivity to various visual and semantic factors), but also to evaluate of learning and long-term memory capacity in typical observers and clinical populations such as patients with semantic dementia or Alzheimer's disease.

Authors' contributions

All authors contributed to the study design. X. Yan and F. Zimmermann collected the data. X. Yan and F. Zimmermann carried out data analysis. X. Yan and B. Rossion drafted the initial manuscript. X. Yan and B. Rossion contributed to the interpretation of the results and manuscript revisions. All authors gave final approval for publication.

Acknowledgments

We thank Holger Wiese and an anonymous reviewer for their critical and helpful comments on previous versions of this manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study was supported in part by a co-funded initiative by the University of Louvain and the Marie Curie Actions of the European Commission award to XY [grant no. F211800013] as



well as a postdoctoral fellowship from the Région Grand Est to XY.

ORCID

Xiaogian Yan http://orcid.org/0000-0003-4711-7428

References

- Adrian, E. D., & Matthews, B. H. (1934). The Berger rhythm: potential changes from the occipital lobes in man. Brain,
- Alsufyani, A., Hajilou, O., Zoumpoulaki, A., Filetti, M., Alsufyani, H., Solomon, C. J., ... Bowman, H. (2018). Breakthrough percepts of famous faces. Psychophysiology, 56(1), e13279.
- Andrews, S., Burton, A. M., Schweinberger, S. R., & Wiese, H. (2017). Event-related potentials reveal the development of stable face representations from natural variability. Quarterly. Journal of Experimental Psychology (Hove), 70(8), 1620-1632.
- Barragan-Jason, G., Cauchoix, M., & Barbeau, E. J. (2015). The neural speed of familiar face recognition. Neuropsychologia, 75, 390-401.
- Barrett, S. E., Rugg, M. D., & Perrett, D. I. (1988). Event-related potentials and the matching of familiar and unfamiliar faces. Neuropsychologia, 26(1), 105-117.
- Benton, A. L., Sivan, A. B., Hamsher, K. D. S., Varney, N. R., & Spreen, O. (1983). Facial recognition: Stimulus and multiple choice pictures. In Benton AL, Sivan AB, Hamsher KDS, Varney NR, & Spreen O. (Eds.), Contribution to neuropsychological assessment (pp. 30-40). New York, NY: Oxford University Press.
- Besson, G., Barragan-Jason, G., Thorpe, S. J., Fabre-Thorpe, M., Puma, S., Ceccaldi, M., & Barbeau, E. J. (2017). From face processing to face recognition: Comparing three different processing levels. Cognition, 158, 33-43.
- Bruce, V. (1982). Changing faces: Visual and non visual coding processes in face recognition. British Journal of Psychology, 73, 105-116.
- Busigny, T., & Rossion, B. (2010). Acquired prosopagnosia abolishes the face inversion effect. Cortex, 46, 965-981.
- Caharel, S., Courtay, N., Bernard, C., Lalonde, R., & Rebaï, M. (2005). Familiarity and emotional expression influence an early stage of face processing: An electrophysiological study. Brain Cognition, 59(1), 96-100.
- Caharel, S., Ramon, M., & Rossion, B. (2014). Face familiarity decisions take 200ms in the human brain: Electrophysiological evidence. Journal of Cognitive Neuroscience, 26, 81-95.
- Collins, E., Robinson, A. K., & Behrmann, M. (2018). Distinct neural processes for the perception of familiar versus unfamiliar faces along the visual hierarchy revealed by EEG. Neuroimage, 181, 120-131.
- Collishaw, S. M., & Hole, G. J. (2000). Featural and configurational processes in the recognition of faces of different familiarity. Perception, 29(8), 893-909.
- Dzhelyova, M., & Rossion, B. (2014a). The effect of parametric stimulus size variation on individual face discrimination indexed by fast periodic visual stimulation. BMC Neuroscience, 15(87), 1-12.
- Dzhelyova, M., & Rossion, B. (2014b). Supra-additive contribution of shape and surface information to individual face

- discrimination as revealed by fast periodic visual stimulation. Journal of Vision, 14(14), 15, 1-14.
- Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behavior Research Methods, 39(2), 175-191.
- Freire, A., Lee, K., & Symons, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. Perception, 29, 159-170.
- Gainotti, G. (2013). Laterality effects in normal subjects' recognition of familiar faces, voices and names. Perceptual and representational components. Neuropsychologia, 51(7), 1151-1160.
- Gilad-Gutnick, S., Harmatz, E. S., Tsourides, K., Yovel, G., & Sinha, P. (2018). Recognizing Facial Slivers. Journal of Cognitive Neuroscience, 30(7), 951-962.
- Huang, W., Wu, X., Hu, L., Wang, L., Ding, Y., & Qu, Z. (2017). Revisiting the earliest electrophysiological correlate of familiar face recognition. International Journal of Psychophysiology, 120,
- Jemel, B., Schuller, A. M., & Goffaux, V. (2010). Characterizing the spatio-temporal dynamics of the neural events occurring prior to and up to overt recognition of famous faces. Journal of Cognitive Neuroscience, 22(10), 2289–2305.
- Jenkins, R., White, D., Van Montfort, X., & Burton, A. M. (2011). Variability in photos of the same face. Cognition, 121(3), 313-323.
- Jonas, J., Jacques, C., Liu-Shuang, J., Brissart, H., Colnat-Coulbois, S., Maillard, L., & Rossion, B. (2016). A face-selective ventral occipito-temporal map of the human brain with intracerebral potentials. Proceedings of the National Academy of Sciences of the United States of America, 113, E4088-E4097.
- Kloth, N., Dobel, C., Schweinberger, S. R., Zwitserlood, P., Bölte, J., & Junghöfer, M. (2006). Effects of personal familiarity on early neuromagnetic correlates of face perception. European Journal of Neuroscience, 24(11), 3317-3321.
- Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2014). An objective index of individual face discrimination in the right occipitotemporal cortex by means of fast periodic oddball stimulation. Neuropsychologia, 52, 57–72.
- Liu-Shuang, J., Torfs, K., & Rossion, B. (2016). An objective electrophysiological marker of face individualisation impairment in acquired prosopagnosia with fast periodic visual stimulation. Neuropsychologia, 83, 100-113.
- Lochy, A., Van Belle, G., & Rossion, B. (2015). A robust index of lexical representation in the left occipito-temporal cortex as evidenced by EEG responses to fast periodic visual stimulation. Neuropsychologia, 66, 18-31.
- Lui, M., Lui, K. F. H., Wong, A. C., & Rosenfeld, J. P. (2018). Suppression of 12-Hz SSVEPs when viewing familiar faces: An electrophysiological index to detect recognition. International Journal of Psychophysiology, 133, 159-168.
- Megreya, A. M., & Burton, A. M. (2006). Unfamiliar faces are not faces: Evidence from a matching task. Memory & Cognition, 34 (4), 865-876.
- Natu, V., & O'Toole, A. J. (2011). The neural processing of familiar and unfamiliar faces: A review and synopsis. British Journal of Psychology, 102, 726–747.
- Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottereau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. Journal of Vision, 15(6), 4, 1-46.



- Quek, G. L., Nemrodov, D., Rossion, B., & Liu-Shuang, J. (2018). Selective attention to faces in a rapid visual stream: Hemispheric differences in enhancement and suppression of category-selective neural activity. *Journal of Cognitive Neuroscience*, 30, 393–410.
- Ramon, M., & Gobbini, M. I. (2018). Familiarity matters: A review on prioritized processing of personally familiar faces. *Visual Cognition*, 26(3), 179-195.
- Ramon, M., Vizioli, L., Liu-Shuang, J., & Rossion, B. (2015). The neural microgenesis of personally familiar face recognition. Proceedings of the National Academy of Science USA, 112, E4835–44.
- Regan, D. (1966). Some characteristics of average steady-state and transient responses evoked by modulated light. *Electroencephalography and Clinical Neurophysiology*, 20(3), 238–248.
- Regan, D. (1989). Human brain electrophysiology: Evoked potentials and evoked magnetic fields in science and medicine. Amsterdam, the Netherlands: Elsevier.
- Retter, T. L., & Rossion, B. (2016). Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. *Neuropsychologia*, *91*, 9–28.
- Rice, G. E., Caswell, H., Moore, P., Lambon Ralph, M. A., & Hoffman, P. (2018). Revealing the dynamic modulations that underpin a resilient neural network for semantic cognition: An fMRI investigation in patients with anterior temporal lobe resection. *Cerebral Cortex*, 1(28), 3004–3016.
- Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychologica*, 128, 274–289.
- Rossion, B. (2014). Understanding individual facediscrimination by means of fast periodic visualstimulation. *Experimental Brain Research*, 232(6), 1599–1621.
- Rossion, B. (2018). Damasio's error-Prosopagnosia with intact within-category object recognition. *Journal of Neuropsychology*, *12*, 357–388.
- Rossion, B., Jacques, C., Torfs, K., & Liu-Shuang, J. (2015). Fast periodic presentation of natural images reveals a robust

- face-selective electrophysiological response in the human brain. *Journal of Vision*, *15*(18), 1–18.
- Rossion, B., & Michel, C. (2018). Normative data for accuracy and response times at the computerized Benton Facial Recognition Test (BFRT-c). *Behavior Research Methods*, *50*, 2442–2460.
- Sekeres, M. J., Winocur, G., & Moscovitch, M. (2018). The hippocampus and related neocortical structures in memory transformation. *Neuroscience Letters*, 680, 39–53.
- Squire, L. R., Genzel, L., Wixted, J. T., & Morris, R. G. (2015). Memory consolidation. *Cold Sping Harbor Perspectives in Biology*, *7*(8), a021766.
- Valentine, T., & Bruce, V. (1986). The effects of distinctiveness in recognizing and classifying faces. *Perception*, 15(5), 525–535.
- White, D., Kemp, R. I., Jenkins, R., Matheson, M., & Burton, A. M. (2014). Passport officers' errors in face matching. *PloS One*, *9* (8), e103510.
- Wiese, H., Tüttenberg, S. C., Ingram, B. T., Chan, C. Y. X., Gurbuz, Z., Burton, A. M., & Young, A. W. (2019). A robust neural index of high face familiarity. *Psychological Science*, 30(2), 261–272.
- Xu, B., Liu-Shuang, J., Rossion, B., & Tanaka, J. (2017). Individual Differences in Face Identity Processing with Fast Periodic Visual Stimulation. *Journal of Cognitive Neuroscience*, *29*(8), 1368–1377.
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81, 141–155.
- Young, A. W., & Burton, A. M. (2018). Are we face experts? *Trends in Cognitive Sciences*, 22, 100–110.
- Zimmermann, F., & Eimer, M. (2013). Face learning and the emergence of view-independent face recognition: An event-related brain potential study. *Neuropsychologia*, *51*, 1320–1329.
- Zimmermann, F., Yan, X., & Rossion, B. (2019). An objective, sensitive and ecologically-valid neural measure of rapid human individual face recognition. *Royal Society Open Science*, *6*, 181904.