



**HAL**  
open science

# A robust neural index of automatic generalization across variable natural views of familiar face identities

Justine David, Laurent Koessler, Bruno Rossion

## ► To cite this version:

Justine David, Laurent Koessler, Bruno Rossion. A robust neural index of automatic generalization across variable natural views of familiar face identities. *Visual Cognition*, 2024, 31 (8), pp.571-583. 10.1080/13506285.2024.2315796 . hal-04724770

**HAL Id: hal-04724770**

**<https://hal.science/hal-04724770v1>**

Submitted on 7 Oct 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Copyright

# A robust neural index of automatic generalization across variable natural views of familiar face identities

Justine David<sup>1</sup>, Laurent Koessler<sup>1\*</sup>, Bruno Rossion<sup>1,2\*</sup>

<sup>1</sup> Université de Lorraine, CNRS, F-54000 Nancy, France

<sup>2</sup> Université de Lorraine, CHRU-Nancy, Service de Neurologie, F-54000 Nancy, France

\*: equal contribution

Correspondence to:

**Bruno Rossion**

CNRS – Université de Lorraine

Pavillon Krug, Hôpital Central, CHRU de Nancy

29 avenue du Maréchal de Lattre de Tassigny

54000 Nancy, FRANCE

bruno.rossion@univ-lorraine.fr

+33 3 83 85 80 53

## Abstract

The ability to automatically and rapidly recognize a familiar face identity across different views is well documented but generally measured with explicit behavioural tasks involving many other processes. Here we provide a sensitive implicit neural measure of this ability using electroencephalographic (EEG) recordings coupled with fast periodic visual stimulation (FPVS). Images of two famous face identities alternated for 15 seconds at a frequency rate of 6 Hz, preceded by a 15 seconds adaptation period to images of one of the face identities. Beyond previous studies, numerous (N=60) non-edited variable natural face images of each identity were presented, with different images appearing at adaptation (N=30) and test. At the group-level (N=16), 3 stimulation sequences only were sufficient to elicit highly significant EEG peaks at odd harmonics (3 Hz and 9 Hz), reflecting face identity discrimination across variable novel views. This response was maximally localized over the right occipito-temporal region and statistically significant in 75% of individuals tested. Importantly, the face identity discrimination response at odd harmonics was significantly larger than when the exact same stimulation sequences were preceded by images of a face identity not present in the alternating sequence (irrelevant adaptation condition). Overall, this study provides a highly sensitive and objective technique to implicitly measure an individual's ability to generalize identity across different views of a familiar face identity.

## Keywords:

Famous face identity recognition; Visual adaptation; Electroencephalography; Fast Periodic Visual Stimulation.

## Introduction

In everyday life human adults automatically and rapidly recognise people's identity across a wide range of viewing conditions of their faces, i.e., variations in head orientation, lighting condition, emotional expressions, etc. Human's excellent ability to generalize across different views of the same familiar face identity has been documented with images for decades (Bruce, 1982; Hill et al., 1997; Bruce et al., 1999; Jenkins et al. 2011; Burton et al. 2016). However, this ability is generally measured with explicit behavioural tasks (e.g., naming, matching tasks), with short or no time constraints (Bruce, 1982; Troje & Kersten, 1999; Young et al., 1986; Megreya & Burton, 2006; Jenkins and al. 2011). For this reason, generalizing across different views of the same face identity may involve many processes (e.g., associating generated names or semantic knowledge, decisional processes, ...) beyond the fast automatic association of visual representations.

Here we aimed at limiting the contribution of these processes by providing an implicit neural index of this ability to rapidly generalize across views of the same familiar face identity using scalp electroencephalographic (EEG) recordings. Previous EEG or MagnetoEncephaloGraphic (MEG) recording studies have shown differences between familiar face identities across variable images (e.g., Schweinberger et al., 2002; Bindemann et al., 2008; Ambrus et al., 2019). However, these studies focus on the time-course definition of these effects, requiring relatively long recording times to obtain group level significant effects only. Moreover, data analysis depends either on arbitrary and variable definitions of time-windows of interest (e.g., Schweinberger et al., 2002; Bindemann et al., 2008) or data-driven multivariate analyses with relatively low power (e.g., Ambrus et al., 2019). Compared to these studies, our goal was to provide a sensitive measure of automatic association of visual familiar face identity representations at the individual level in a short amount of time. To achieve this objective, we coupled EEG with frequency-tagging, or fast periodic visual stimulation (FPVS), focusing on neural responses in the EEG frequency-domain. While precise time-domain information may be more difficult to extract in some FPVS paradigms due to the overlap of responses of interest to successive relevant stimuli (see Retter & Rossion, 2016b), the approach is characterized by substantial advantages in terms of objectivity (i.e., pre-defined frequencies of interest to measure a neural response usually in a small frequency bin) and sensitivity (i.e., high signal-to-noise ratio, SNR).

Specifically, here we used a symmetry/asymmetry visual stimulation characterized by the repetitive alternating presentation of two stimuli at a fixed frequency rate (Victor & Zemon, 1985). In this stimulation condition, two stimuli eliciting the same neural activity lead to a response only at the stimulation rate (e.g., 6 Hz), while a differential neural activity between the alternating two

stimuli should lead to an additional asymmetrical EEG response at half the stimulus repetition frequency (i.e., 3 Hz in this case; e.g., Ales & Norcia, 2009; see Norcia et al. 2015).

Such symmetry/ asymmetry paradigms coupled with periodic visual stimulation in EEG have long been used to differentiate low-level visual representations (e.g., motion direction; contrast; Cobb, Morton, & Ettlinger, 1967; Spekreijse, van der Tweel, & Zuidema, 1973) and more recently high-level visual representations (i.e., a face structure; Ales et al., 2012; Liu-Shuang et al., 2015). However, considering the low spatial resolution of scalp EEG, even if different neural populations respond preferentially to each representation (e.g., motion directions), the measure obtained at the population level on the scalp is not different between these representations (of motion directions), leading to an absence of asymmetrical response. Therefore, to produce an asymmetry between underlying neuron responses, it is necessary to use selective adaptation to one of the stimuli (e.g., Tyler & Kaitz, 1997; Ales & Norcia, 2009; Norcia et al., 2015), causing an asymmetry in the neural response between adapted and unadapted stimuli.

Based on this principle, Retter and Rossion (2016b) combined adaptation with a FVPS-EEG symmetry/asymmetry paradigm to study unfamiliar face identity discrimination. In that study, participants were adapted during 10 seconds (s) to a segmented full-front picture of an unfamiliar face identity alternating with another identity at a rate of 6Hz. Following relevant adaptation, only for upright faces, a specific EEG response was found at the asymmetry frequency ( $6\text{Hz}/2= 3\text{Hz}$ ) over the right occipito-temporal region (Lithfous & Rossion, 2018; Retter & Rossion, 2016b; see also Retter & Rossion, 2017). Compared to behavioural measures in explicit tasks, this implicit neural measure of face identity discrimination has several advantages. First, stimulus presentation frequency is set in advance by the experimentalist and the EEG response is expected exactly at this frequency rate following frequency domain analysis, providing objectivity (Regan, 1989 and Norcia et al. 2015 for a review). Second, participants are not aware of what is being measured, with only an orthogonal task used to maintain their attention. Last, the high frequency rate of visual stimulation (166.67 ms/image) enable to measure fast face identity recognition (i.e., one fixation by face image), strongly reducing the reliance on nonvisual associations between repeated presentations of the same stimulus.

In the present study, we extend this approach for the first time to measure the implicit ability of generalization across viewing conditions for a familiar face identity. In our study, two familiar (i.e., famous) face identities are presented alternatively at a frequency rate of 6Hz, preceded by an adaptation period to either one of the two alternating face identities (adaptation condition) or another identity not present in the alternating sequence (control condition). Beyond the use of

familiar faces, compared to the study of Retter and Rossion (2016b) (and all other studies using this approach to our knowledge), the present study is original at three levels. First, we use natural (i.e., unsegmented, ‘ambient’) images of faces. Second, rather than using only two alternating images, we use a large set (N=60) of images varying in size, expression, lighting, and head orientation for each identity (Figure 1). In these conditions, the generation of an asymmetric EEG response truly depends on the ability to generalize across views of the same face identity. Last but not least, for the adapting face identity, strictly *different* sets of natural images of that identity are presented during the adaptation and testing time periods (**Figure 1**), strengthening the requirement for generalization across views.

Even in these highly challenging conditions, we hypothesised that participants would be able to automatically generalize across the different views of a face identity, leading to an adaptation effect and thus an asymmetrical EEG response. To ensure that this putative asymmetrical EEG index of familiar face identity recognition was due to adaptation (rather than intrinsic differences in neural activity between the two alternating identities), a control condition with an irrelevant adaptation (i.e., variable images of a third identity) was also included in the study (**Figure 1**).

## Materials and methods

### 2.1 Participants

Sixteen healthy individuals (mean age:  $24.8 \pm 4.9$ ; 3 males) took part in the experiment. All participants were right-handed and had normal or corrected-to-normal vision. The number of participants was determined based on previous FPVS-EEG studies of human face identity recognition (since Rossion & Boremanse, 2012, N=12), in particular with the symmetry/asymmetry paradigm as used here (Litfous & Rossion, 2018: N=14; Retter and Rossion, 2016b: N=16; Retter and Rossion, 2017: N=22). While this may be considered as a relatively low sample of participants, the technique is associated with high sensitivity (i.e., SNR), in part due to the high number of trials (135 discrimination of identities per condition for each participant, see below), allowing data to be analysed statistically also at the single participant level, beyond group-level analyses.

None of the participants had reported to have a history of neurological or psychiatric disorder. All participants performed the electronic version of the Benton Face Recognition Test (BFRT-c, Rossion & Michel, 2018) with a mean score of 43.4/54 ( $\pm 4.2$ ) and mean total response time (RT) of  $156.25 \pm 36$  sec. They gave signed, informed consent prior to the experiment, which was approved by the Ethical Committee Ile de France X (n° 2021-A02807). All participants received monetary compensation for their participation.

### 2.2 Stimuli

Nine facial identities, divided in three groups, were used. Each group was composed of three celebrities selected according to their popularity/familiarity among the French adult population (Group 1: *Patrick Bruel (PB)*, *Jean Dujardin (JD)*, *Tom Cruise (TC)*; Group 2: *Claire Chazal (CC)*, *Angela Merkel (AM)*, *Marine Le Pen (MP)*; Group 3: *Nicolas Sarkozy (NS)*, *Emmanuel Macron (EM)*, *Manuel Valls (MV)*) (see Suppl. Materials, Fig. 1). In each group, the first ones (i.e., *Patrick Bruel or Claire Chazal or Nicolas Sarkozy*) was used as the adapted identity (Figure 1), the second one (*Jean Dujardin or Angela Merkel or Emmanuel Macron*) was used as the alternative identity, and the last one (*Tom Cruise or Marine Le Pen or Nicolas Sarkozy*) as the irrelevant identity. For each of the alternative and irrelevant identities, 30 natural variable images were used. For the adapted identity, 30 natural images for the adaptation phase and 30 other natural images were used for the alternation sequence (i.e., 60 images in total). Images varied substantially in lighting conditions, head orientation, facial expression, etc. (**Figure 1**). As in Ambrus et al. (2019), a structural similarity index measure (SSIM; Wang et al., 2004) was computed for each identity using 10 000 iterations of randomly selected paired of images comparison. The mean SSIM were: PB: 0.276, JD: 0.320, TC: 0.327, CC: 0.575, AM: 0.564, MP: 0.406, NS: 0.273, EM: 0.317, MV: 0.301, reflecting the high variability across images of a same identity. Most importantly, using this index, image variability between alternated identities was similar to image variability within identity (PB-JD: 0.271; AM-CC: 0.553; NS-EM: 0.276). The faces identities in each group were selected to be similar in general physical appearance (age, hair colour, no distinctive facial feature such as a mole, etc.). All images were resized to 200 × 250 pixels, but face size could vary across images due to a variable amount of background. Displayed on a LED monitor (BenQ XL2420T) with a refresh rate of 60Hz and 1920 × 1080 window resolution at a distance of 80 cm from the participant, the stimuli subtended a visual angle of approximately 9.1° in height and 8.5°.

### 2.3 Procedure

The experiment was run in a quiet and low-lit room. After, administering preliminary questionnaires and preparing the EEG recording (about 45 minutes (min) in total), the participant was seated in front of a computer monitor and a computer keyboard. As indicated in the introduction, the paradigm was adapted from previous studies measuring visual adaptation to facial identity (Retter & Rossion, 2016b, 2017), but with unsegmented natural familiar faces. It consisted of six stimulation sequences of 34 s each, for a total testing time of only about 4 minutes with short breaks given between sequence. During all stimulus presentation, the stimuli were shown at a constant rate of 6 images per second (6 Hz) by means of square-wave modulation of contrast (with a 50% duty cycle, e.g., Retter et al., 2018). The structure of each stimulation sequence was the same across conditions (Figure 1). Each sequence began with 2-5 s of grey background and a 2 s stimulus fade-in, during which the maximum stimulus contrast gradually increased to 100%, in order to

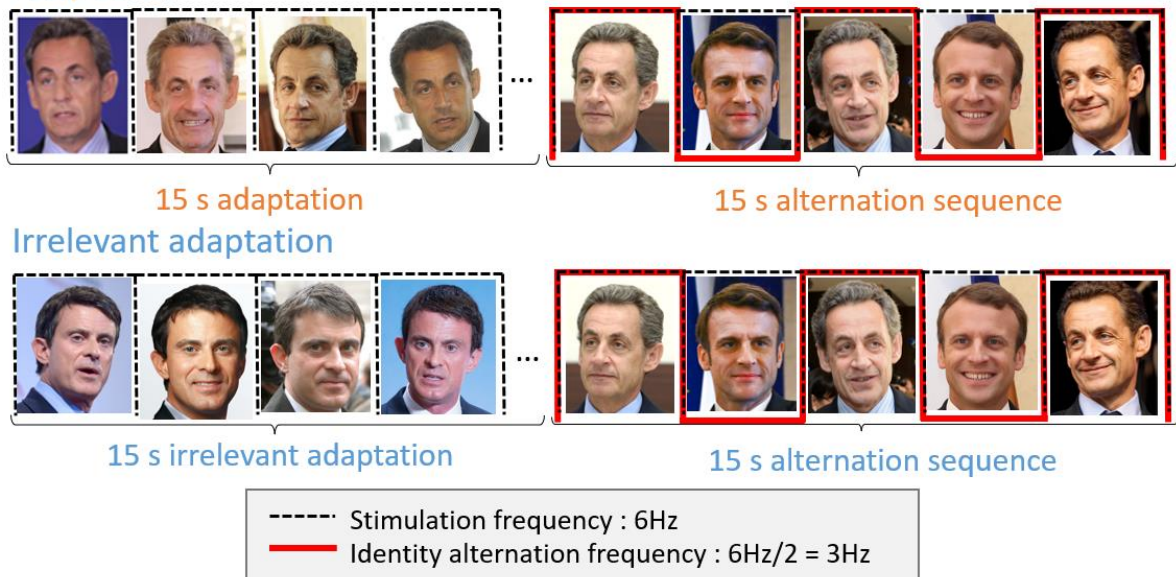
reduce expectation and behavioural reaction (e.g., blinks) to sudden stimulus-onset. Then, there was a 15 s adaptation baseline, in which 30 different images of the same facial identity were presented at 6 Hz (i.e., 1 image every 166.7ms), followed by the testing sequence of 15 s of alternation of two facial identities (for an identity repetition rate of 3 Hz, i.e., 6Hz/2, corresponding to 333 ms). Overall, in comparison to standard event-related potential (ERP) experiments, this procedure leads to 45 trials (i.e., alternations of identities) per sequence (15 sec\*3 repetitions per second), for a total of 270 trials per participants (45\*6 sequences). Finally, to similarly gradually end each sequence, there was a 2 s stimulus fade-out and 2 s of the grey background.

Two experimental conditions were compared (3 stimulation sequences each). In the *adaptation* condition, one facial identity from the alternation sequence pair was presented during the adaptation baseline (30 different images). In the irrelevant adaptation condition, another facial identity (irrelevant face) not present in the alternation sequence was used during the adaptation baseline. Crucially, stimuli presented in the alternation sequence were the same between the two conditions, with the only difference being the order of presentation of the image that was randomized between sequence. Only one group of three face identities was used by sequence, with two sequences for each group. As mentioned above, another critical aspect of the paradigm is that in the adaptation condition, different stimuli were used between the adaptation sequence and the alternation sequence. Stimulation sequence order was fully randomized for each participant.

During each sequence, participants' task, to encourage constant attention, was to attend to the image displayed on the computer monitor and to press on the space bar when the two vertical bars surrounding the image briefly change colour (from black to white), but not to press when only one bar change colour (to avoid that participants focused on only one side of the stimulus) (e.g., as used in Yan et al., 2022). Participants were instructed to pay attention to the centrally presented faces during the bar task. These colour changes occurred 8 random times within each trial. Behavioural accuracy was calculated by dividing the sum of the hits (when the participant presses the space bar up to 1 s after the bar change colour) and correct rejection (when the participant does not press the bar after only one bar changes colour) by the total number of changes. Mean accuracy were close to ceiling in each condition (adaptation : M = 97%, SE = 2.9%; irrelevant adaptation : M = 94%, SE = 3.9%) and they were no significant difference in response time across condition (adaptation : M = 536 ms, SE = 70 ms; irrelevant adaptation : M = 546 ms, SE = 67 ms;  $U=37, p=.12, r=0.4$ ).



## Adaptation



**Figure 1 Caption:** Schematic illustration of the experimental design (group 3 faces). Images are presented at a fixed rate of 6Hz (i.e., 6 images by second). The two conditions are identical except that in the adaptation condition one of the two identities presented in the alternance sequence has been presented for 15s before (different images). If adaptation to one of the identities present in the alternance sequence produces an effect, there should be an asymmetry in the response at the rate of alternation, i.e., 3 Hz. The three celebrity faces shown in the figure are Nicolas Sarkozy (Pictures licensed under the CC BY-NC-ND 2.0. Attribution: UMP Photos; CC BY 4.0. Attribution: 首相官邸, Kremlin.ru; CC BY 2.0. Attribution: European People's Party, MEDEF; CC BY-SA 2.5 Attribution: Aleph) Emmanuel Macron (Pictures licensed under the Creative Commons Attribution-ShareAlike 4.0 International. Attribution: Kobi Gideon / Government Press Office; CC BY 2.0. Attribution: EU2017EE Estonian Presidency) and Manuel Valls (Pictures licensed under the CC BY-SA 2.0. Attribution: Press Cambrabcn; CC BY-NC-ND 2.0. Attribution: Jean-Phillippe Baltel, Phillippe Grangeaud; CC BY-SA 4.0. Attribution: Pablo Tupin-Noriega). Image used in the experiment are not those shown in the figure due to copyright reasons.

After EEG recording, participants were asked to complete a questionnaire to check their knowledge about the famous faces used in the experiment. In the questionnaire, each of the 9 faces identities presented during the experiment (new pictures) were shown, together with 10 unfamiliar identities. The participants had to respond whether the face identities were familiar to them (yes, no, uncertain), and if the face was familiar, the participants were required to rate its familiarity on a 10-point Likert scale (from “rarely seen in the media” to “very frequently seen in the media”) and report its name and occupation. On average, the participants were familiar with 8.26 ( $\pm 0.99$ ) out of 9 familiar faces (91.8%  $\pm 11.08$ ). The mean familiarity ratings to the faces presented in the EEG experiment was 8.36 ( $\pm 1.8$ ).

### 2.4 EEG acquisition

High-density 128-channel EEG was recorded with a BioSemi ActiveTwo system (Biosemi, Amsterdam, The Netherlands). Offsets of the electrodes, referenced to the common mode sense (CMS), were held below 30 mV. Three flat-type Active-electrodes were used to record electrooculogram (EOG): one above the participant right eye and two laterals to the external canthi of the two eyes. The EEG and EOG were digitized at a sampling rate of 512 Hz.

### 2.5 EEG analysis

EEG analysis was performed with *Letswave 6*, an open-source toolbox (<https://www.letswave.org/>) running over MATLAB R2021a (MathWorks, USA), with similar data processing steps as previous studies (e.g., Retter & Rossion, 2016b).

### 2.5.1 Preprocessing

First, a single EEG data file was imported for each participant. The data were then filtered using a Butterworth band-pass filter with a cut-off value of 0.1-100 Hz, and a Fast Fourier Transform (FFT) multi-notch filter with a width of 0.5 Hz to remove electrical noise at 50 Hz frequency and 2 harmonics (100 and 150Hz). After being downsampled to 256 Hz to reduce computational load and storage space, data were segmented by sequence, including 2 s before and after the sequence (-2 to 36 s). Eyeblink correction was applied on participant who blink more than 0.2 times/s on averaged during the sequence (Retter & Rossion, 2016b) with independent component analysis (ICA), removing only one clear component (in 7 participants). Individual channels with artifacts (0-2 channels per participant; 0.5% of channels on average) were interpolated with pooled three neighboring channels. All EEG channels were re-referenced to a common average reference.

Each sequence was then re-segmented with an integer number of 3Hz cycles starting after the adaptation baseline (17 s). The resulting cropped epochs were 14.68 s long and contained exactly 44 cycles of 0.33 s. Epochs of a same condition were averaged for every participant. Then, to represent the data in the frequency domain, a Fast Fourier Transform (FFT) was applied, and the amplitude spectra were extracted, with a frequency resolution of 0.068 Hz (1/14.68 s). Grand average spectra were computed to display results at the group level.

Three regions-of-interest (ROIs) were selected based on both previous studies (Retter & Rossion, 2016b, 2017) and on the observed scalp topographies: the right occipito-temporal (ROT) ROI, the homologous left occipito-temporal (LOT) ROI and the medial occipital (MO) ROI. Each region was made up of five channels: PO10, P10, PO12, P8, PO8 (ROT); PO9, P9, PO11, P7, PO7 (LOT) and PPOz, POz, POOz, Oz, Oiz (MO). Amplitude response on each ROI was computed by averaging the signal of the five electrodes making up the ROI. Based on previous results, it was predicted that the 3Hz alternation response would be present in the adapted condition maximally at ROT ROI, while the 6Hz stimulation frequency, a mixture of low-level and high-level (face-related) visual activity, would be maximal at MO ROI (Retter & Rossion, 2017; Lithfous & Rossion, 2018) in both conditions.

In order, to identify significant responses at the frequency of interest and harmonics, we calculated Z-scores ( $Z = (x - \text{baseline}) / \text{standard deviation of the baseline}$ ) across the ROIs of the grand average spectrum. Z-scores were computed using a baseline of the sixteen surrounding bins excluding the immediately adjacent bin (corresponding to a frequency range of 1.09 Hz). Responses

were considered significant if the Z-score was above 2.32 ( $p < .01$ ), indicating that the response was significantly larger than the EEG noise estimated in the neighbouring frequencies. This procedure was used to select the number of harmonics to consider for further analyses. Significant harmonics were determined using the ROI associated with the largest response. Subsequent analyses were performed using the sum of the significant harmonics (Retter & Rossion, 2016b; Retter et al., 2021).

Two methods were used for baseline correction to account for differences in baseline noise across the frequency spectrum at the individual level: (1) a division by the EEG noise to display EEG spectra in signal-to-noise ratio (SNR) and (2) a subtraction of the EEG noise (baseline subtraction, SBL) to quantify responses in  $\mu\text{V}$ . For both, EEG noise was calculated by averaging the sixteen surrounding bins, excluding the immediately adjacent bins (in case of spectral leakage) and the local maximum and minimum amplitude bins (to avoid creating 'dips' in the EEG spectra around the peaks of activity). These baselines corrected spectra were grand-average across subjects for display at the group level.

To investigate adaptation effect at the individual level, the number of significant electrodes was calculated for each subject by computing a Z-score on each electrode amplitude for every subject and for each condition.

Statistical analyses were done to compare conditions and ROIs. Two-way repeated measures ANOVAs were computed on baseline-corrected amplitudes, with factors of *Condition* (two levels: adaptation and irrelevant adaptation) and *Region* (three levels: MO, ROT, LOT). When Mauchly's test of sphericity was significant, a Greenhouse-Geisser correction was applied to the degrees of freedom. Multiple comparisons were performed using pairwise T-test with Bonferroni correction.

### 2.5.2 Temporal evolution of the adaptation effect

To investigate the evolution of the adaptation over time, we segmented the alternation sequence into successive 3 seconds segments, corresponding to 5 epochs. Segmentation was done in the re-referenced file for each subject. Segments were then averaged by condition and FFT was applied with a frequency resolution of 0.33 Hz. A SNR baseline-correction was computed in the same way as above except that given the lower frequency resolution, the baseline noise was defined as only the 2 surrounding bins after excluding the immediately adjacent bin and the local maximum and minimum amplitude bin. Pairwise t-test were computed on each segment to compare response amplitudes between the two conditions.

## Results

### 3.1 Face stimulation response (symmetry frequency or even harmonics)

As expected, both conditions gave rise to a large response at the face stimulation rate of 6 Hz (Figure 2A) and harmonics (12 Hz, 18 Hz, etc. not shown). Responses were significant up to 10 harmonics in the MO ROI (all Z-score > 3.1,  $p < .001$ ). The sum of the response at 6 Hz and harmonics quantified for the average of all EEG channels was significant for both conditions (*adaptation*:  $Z=52.11$ ,  $p < .001$ ; *irrelevant adaptation*:  $Z=42.96$ ,  $p < .001$ ). As predicted, this response was present maximally over the MO ROI (Figure 2 A&B). Statistical analyses revealed no main effect of *Condition* ( $F_{(1,15)} = 2.33$ ;  $p = .15$ ;  $\eta^2 p = .13$ ). There was a significant effect of *ROI* ( $F_{(2,30)} = 13.02$ ;  $p < .001$ ;  $\eta^2 p = .46$ ) with post-hoc test showing that the response was larger for the MO ROI ( $3.64 \pm 0.25$ ) than for the LOT ROI ( $1.91 \pm 0.13$ ),  $p < .0001$  and larger for the ROT ROI ( $3.05 \pm 0.28$ ) than for the LOT ROI,  $p < .001$ , but the difference of the response amplitude was not significant between MO and ROT ROIs,  $p = .067$ .

### 3.2 Face identity discrimination (asymmetry frequency or odd harmonics)

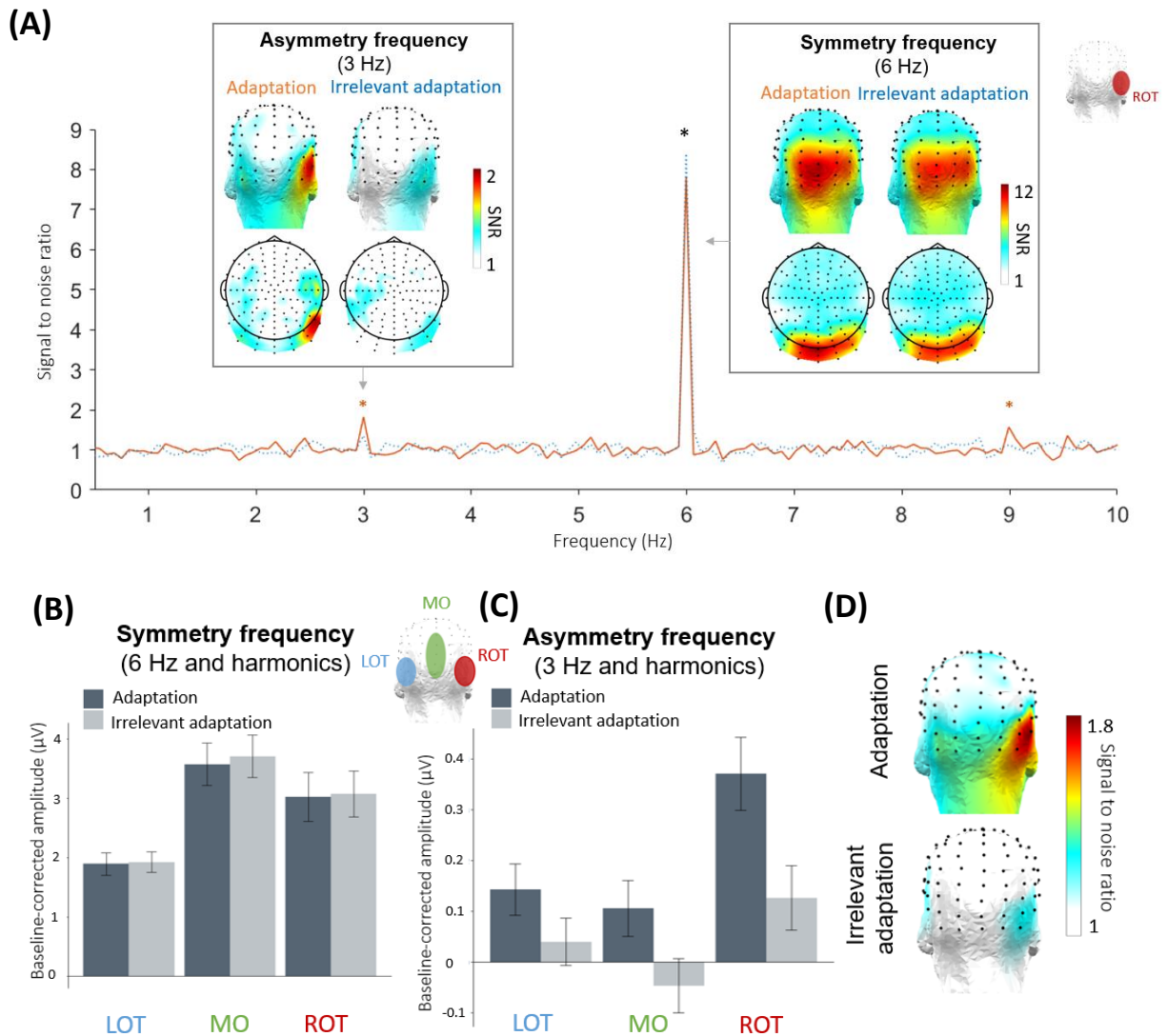
A distinct EEG peak was present at 3 Hz in the EEG spectrum, particularly prominent over the right occipito-temporal region (ROT), in the adaptation condition (Figure 2A). This 3 Hz response in the adaptation condition reaches a SNR of 1.9, which corresponds to 90% increase of signal. Interestingly, there was also a distinctive smaller peak at the third harmonic (9 Hz), visible only in the adaptation condition (Figure 2;  $SNR = 1.6$ ).

Statistical analyses revealed a highly significant response at the first two harmonics at the ROT ROI in the adaptation condition (3Hz:  $Z = 5.3$ ,  $p < .001$ ; 9Hz:  $Z = 3.49$ ,  $p < .001$ ), with the first harmonic accounting for 71% of the response. In the irrelevant adaptation condition, only the first harmonic (3 Hz) was significant (3Hz:  $Z = 3.07$ ,  $p < .01$ ; 9Hz:  $Z = 1$ ,  $p > .05$ ). There were no visible or significant peak at higher odd harmonics (i.e., 15Hz, 21Hz, etc.;  $p > .05$ ) in the EEG spectrum of any of the two conditions. Thus, all subsequent analysis was done on the summed amplitude of the two harmonics at 3 Hz and 9 Hz, taking into account the whole periodic EEG response (Retter et al., 2021).

This asymmetry frequency response over the ROT ROI was significant for both conditions (*adaptation*:  $Z = 7.96$ ,  $p < .001$ ; *irrelevant adaptation*:  $Z = 3.05$ ,  $p < .01$ ) but the amplitude was much (i.e., 2.47 times) larger in the adaptation ( $0.388 \pm 0.078 \mu V$ ) than the irrelevant adaptation condition ( $0.157 \pm 0.065 \mu V$ ). The response was also significant for the LOT ROI and MO ROI but only in the adapted condition (LOT:  $Z = 2.36$ ,  $p < .01$ ; MO:  $Z = 1.85$ ,  $p < .05$ ; irrelevant adaptation condition: LOT:  $Z = 0.74$ ,  $p > .05$ ; MO:  $Z = -0.79$ ,  $p > .05$ ) and with a weaker amplitude (LOT:  $0.132 \pm 0.051 \mu V$ ; MO:  $0.09 \pm 0.054 \mu V$ ). The response was not significant for the average of the 128 channels neither for the

adapted condition ( $Z=1.38$ ,  $p>.05$ ) nor for the irrelevant adaptation condition ( $Z=0.18$ ,  $p>.05$ ), and there was no evidence of any channel showing a larger response anywhere on the scalp for the irrelevant adaptation condition (Figure 2).

Statistical comparison of the quantified asymmetry frequency response between conditions revealed a significant main effect of *Condition* ( $F_{(1,15)}= 5.99$ ;  $p<.05$ ;  $\eta^2p=.29$ ) and a significant main effect of *ROI* ( $F_{(2,30)}= 11.98$ ;  $p<.001$ ;  $\eta^2p=.44$ ). There was no significant interaction between these factors ( $F_{(2,30)}= 1.77$ ;  $p=.19$ ;  $\eta^2p=.11$ ). Post hoc pairwise comparisons with Bonferroni correction for the factor *ROI* showed that the ROT ROI produced a significantly higher response ( $0.27\pm 0.05 \mu\text{V}$ ) than either the LOT ROI ( $0.09\pm 0.035\mu\text{V}$ ,  $t_{31}=3.2$ ,  $p<.01$ ,  $d=0.57$ ) or the MO ROI ( $0.03\pm 0.036 \mu\text{V}$ ,  $t_{31}=5.3$ ,  $p<.0001$ ,  $d=0.94$ ). There were no significant differences between LOT ROI and MO ROI ( $t_{31}=1.6$ ,  $p=.4$ ,  $d=0.3$ ). For the factor *Condition*, post hoc t-test showed a significant difference between the adaptation condition and the irrelevant adaptation condition ( $t_{47}=3.3$ ,  $p<.01$ ,  $d=0.48$ ).



**Figure 2 Caption:** (A) Frequency-domain signal-to-noise (SNR) spectra at the group level of the average of the five electrodes composing the right occipito-temporal (ROT) region-of-interest (ROI) (PO10, P10, PO12, P8, PO8) for the two

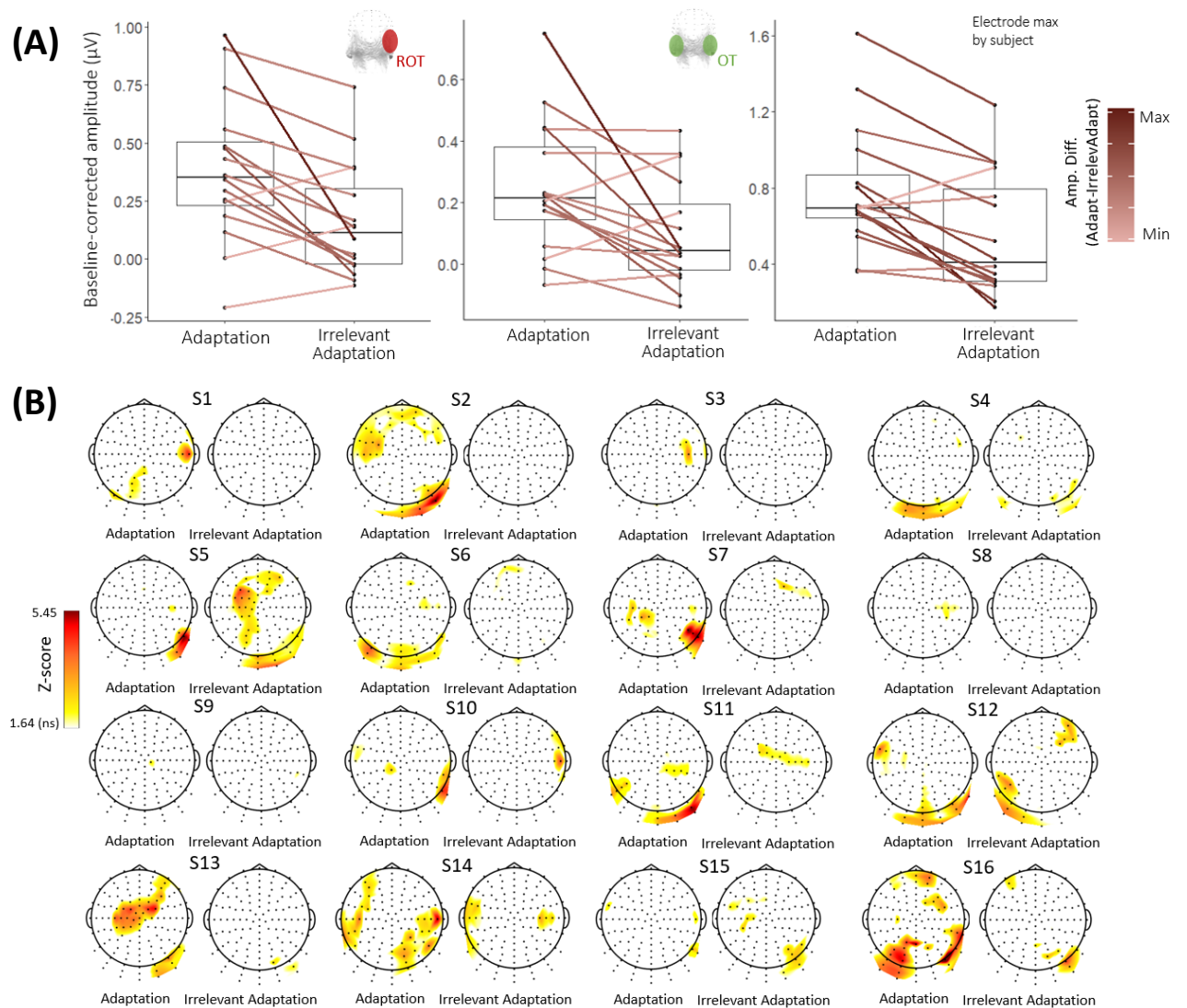
experimental conditions (adaptation condition in orange and irrelevant adaptation condition in blue). Here a response at 3Hz is observed, corresponding to the asymmetrical responses to facial identities alternation, larger for the adaptation condition. A very large response amplitude is also present at 6Hz, corresponding to the visual stimulation presentation frequency, with no difference between conditions. In the scalp topographies of the 3Hz response shown above, the largest activity is present in the ROT ROI for adaptation condition while the scalp topographies of the 6Hz response show maximal activation in occipito-medial region. Asterisks indicate significant amplitude responses. (B) Quantification of the mean responses for the 16 participants at each of the three ROIs in terms of baseline-subtracted amplitude at the (B) stimulation presentation frequency (6Hz) and (C) identity alternation frequency (3Hz) for both the adaptation (dark grey) and irrelevant adaptation condition (light grey) with error bars representing one standard error above and below the mean. (D) SNR scalp topographies display for the sum of significant odd harmonics frequency (3Hz & 9Hz).

### 3.3 Individual participants

Analyses ran at the individual participant level showed a significant amplitude of the summed 3 Hz and harmonic (9Hz) response across at least one ROI for 75% of participants (i.e., N=12) in the adaptation condition. Among those participants, this response was maximally localized over the ROT ROI for 10 participants, over the MO ROI for one participant and over the LOT ROI for one participant (Figure 3). In the irrelevant adaptation condition, only 37.5% of participants (N=6 participants) had a significant response. Comparison between the two conditions on each participant revealed a larger amplitude in the adaptation condition than in the irrelevant adaptation condition for 13 participants in the ROT ROI. Since a few participants also had a strong response at left occipito-temporal sites (Figure 3), we also combined both occipito-lateral ROIs (ROT and LOT). In this case, 11 participants had a larger amplitude in the adaptation condition than in the irrelevant adaptation condition. Comparison performed with the maximal amplitude electrode by participant for each condition shows a larger amplitude in the adaptation condition for 13 participants. The electrode with the maximal response fell in the defined ROI for 10 participants in the adaptation condition and 8 participants in the control condition.

At the individual level, we also considered the number of significant electrodes ( $Z > 1.64$ ,  $p < .05$ ) per condition for each participant (Figure 3B). In the adaptation condition, 13 individuals had more significant electrodes than chance level (i.e.,  $0.05 * 128 = 6.4$ ). There was also larger number of significant electrodes in the adaptation condition compared to the control condition for 13 individual participants out of 16 (81.25%) (Figure 3B).

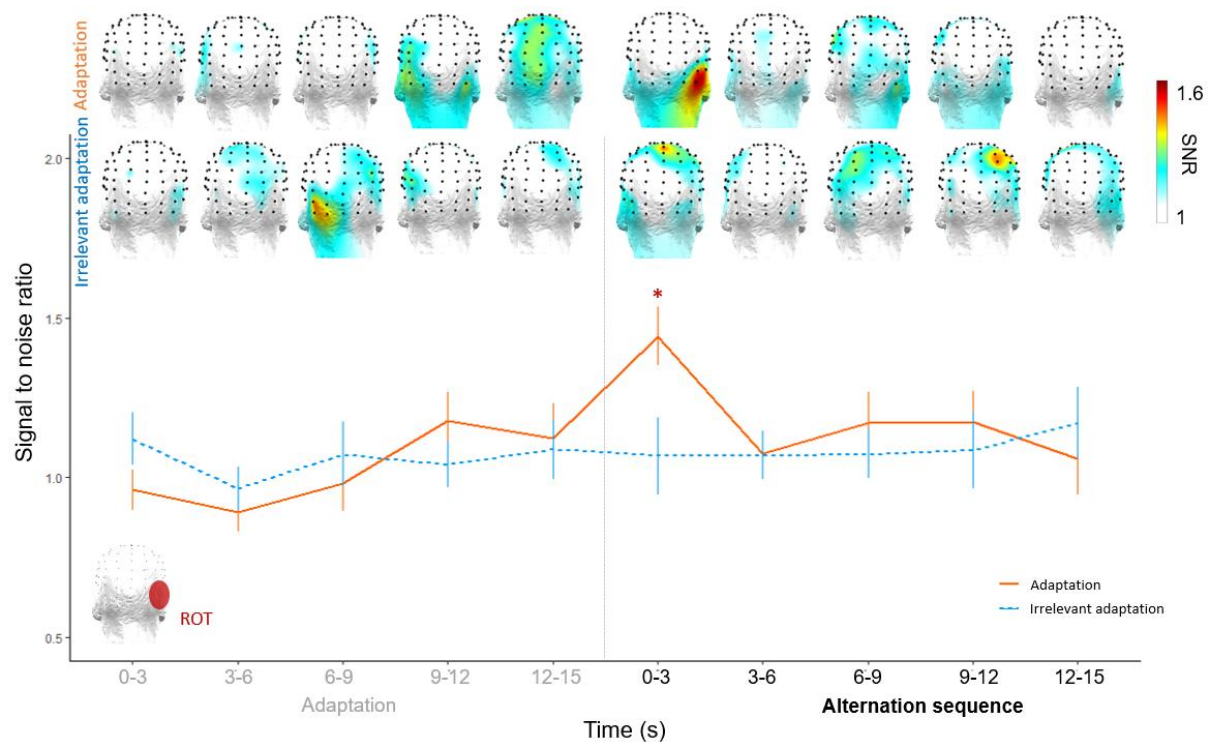




**Figure 3 Caption :** (A) Comparison of the baseline-corrected amplitude between the adaptation condition and the irrelevant adaptation condition. Each point representing a participant. Values corresponding to the same subject are joined by a line. For the ROT ROI on the left, the OT ROI in the middle and for the subject's maximum amplitude electrode by condition on the right. Colour of the line correspond to the size of the amplitude difference between the two conditions (darker red representing a larger difference). (B) Individual 2D (top view) scalp topography of significant Z-scores distribution for both conditions and for every subject. White corresponds to non-significant response.

### 3.4 Temporal evolution of the adaptation effect

At the group level, the asymmetry frequency response at 3Hz (and harmonic) was present for the adaptation condition only during the first 3 seconds immediately following the adaptation sequence but not present during the rest of the sequence (Figure 4). Comparison of the corrected amplitude at the ROT ROI between the two conditions for each 3 s segment revealed a significant difference only for the first 3 seconds segment immediately following the adaptation sequence ( $t(15)= 2.22, p<.05$ ; all others  $p's>.05$ ). In contrast, at 6Hz, no significant difference between the two conditions was found for each 3 seconds segments at MO ROI or at ROT ROI (all  $p's>.05$ ).



**Figure 4 Caption :** Temporal evolution of the 3Hz response quantified with signal to noise ratio at ROT ROI, in orange for adaptation condition and in blue for irrelevant adaptation condition. The red star indicates that difference of amplitude between the two conditions was significant only for the first 3 second segment immediately following the adaptation. Scalp topographies of the response are shown above to depict the localisation of the response.

## DISCUSSION

Here we demonstrate that a 15 s adaptation period to a famous face identity with varying natural images produces a significant increase of an asymmetrical (odd harmonics) 3 Hz EEG response during the alternation of this identity with another one. These results replicate those of Retter and Rossion (2016b, 2017), extending them significantly to variable natural images and the use of different images between the adaptation and test sequences. Therefore, in the present study the EEG adaptation effect does not only reflect the identity discrimination process but also generalization across different views of a same familiar face identity.

As mentioned in the introduction, the ability to generalize across different views of the same familiar face identity is well documented in behavioural studies (Bruce, 1982; Hill et al., 1997; Bruce et al., 1999; Burton et al. 2016), including studies that relied on a large number of variable natural images of the same face identity (Jenkins et al. 2011). In terms of neural signals, generalization across views of familiar (and unfamiliar) face identities has been mainly investigated with functional magnetic resonance imaging (fMRI) in face-selective regions of the occipito-temporal cortex, with stimulus sets that are much less natural (i.e., edited, all full-front, often cropped images, without background and in greyscale) and variable (in terms of number of images per face and their degree of variability) than used here. It is fair to say that these studies have led to relatively inconsistent



results (e.g., Eger, Schweinberger, Henson, & Dolan, 2005; Pourtois et al., 2005; Ewbank & Andrews, 2008; Davies-Thompson, Gouws, and Andrews, 2009; Davies-Thompson et al., 2013; Weibert et al., 2016). Findings in EEG (or MEG) studies focusing on time-domain EEG analyses (event-related potentials, ERPs) of immediate stimulus repetition paradigms have been more consistent at the group level, especially for the N250 repetition effect (N250r; e.g., Schweinberger et al., 2002; Bindemann, Burton, Leuthold & Schweinberger, 2008). However, compared to these studies, the stimulus set used here holds substantial advantages in terms of naturalness and variability (i.e., 60 images per adapted face identity in total). Most importantly, as mentioned in the introduction section, compared to these EEG approaches, here our goal was not to define the time-course of such effects, but to provide an objective and sensitive measure of automatic association of visual face identity representations at the individual level in the EEG frequency-domain, within only a few minutes of recording.

Interestingly, the 3Hz asymmetric response was also significant in the irrelevant adaptation condition used here, but with a significantly weaker amplitude than in the adaptation condition. In the former case the 3 Hz response cannot be due to adaptation because the participant was not adapted to any of the two alternating identities. This significant EEG response in the irrelevant adaptation condition reflects familiar face identity discrimination without adaptation (as in Ambrus et al., 2019) and could be accounted for by several factors. For instance, despite the large variability of views of the same face identity, systematic visual differences between the two alternated faces (e.g., one identity having darker hair than the other) could generate a 3 Hz response. Participant's level of familiarity or emotional association to one of the two famous identities (e.g., being a fan of Jean Dujardin) could also induce a specific neural response for one of the two identities. Moreover, since familiar faces differ also at the semantic level (e.g., Claire Chazal is a TV presenter while Angela Merkel is a politician), this could have also induced an asymmetrical neural response. In future studies, the paradigm could be further improved by more stringently controlling for visual differences between stimulus sets, like homogenise semantic categories and level of familiarity/emotional associations in each group or yet by counterbalancing the identities used for adaptation between participants to make any potential identity-specific effects less likely. However, and critically, the larger 3Hz amplitude response present in the adaptation condition cannot be due to those factors because the same images are used in both conditions for the alternance sequence.

As in previous studies, a strong 6Hz response was found in both conditions, reflecting neural activity common to both stimuli. There was no significant difference between the two conditions for this symmetrical response, implying no low-level visual difference and no difference in participant attention between conditions, as also supported by the attentional task results (see Material and Methods). This 6 Hz response was prominent over the occipital pole, while the 3 Hz

response was maximally localized over the right occipito-temporal region, which correspond to the localization of brain regions implicated in human face recognition, in particular face identity recognition (Sergent et al., 1992; Bentin et al., 1996; Rossion et al., 2015; Jacques et al., 2020).

Unlike these latter studies, here we did not investigate the adaptation effect with unfamiliar faces. Since it is more challenging for humans to generalize identity for unfamiliar faces (Hancock, Bruce & Burton, 2000; Johnston & Edmonds, 2009; Burton et al. 2016), the adaptation effect would have been certainly lower with unfamiliar faces or would have taken more time to emerge (i.e., longer adaptation period and more trials). It would be very interesting in future studies to compare familiar with unfamiliar identity faces with the present FPVS-EEG adaptation paradigm.

Analysis of temporal dynamic of the adaptation effect revealed a very short duration of this effect (3 s). This is consistent with previous studies (Retter & Rossion, 2016b, 2017) and with findings from behavioural studies, showing that the amplitude of the adaptation effect is inversely correlated with the test duration time (Leopold et al. 2005). Importantly, Lithfous & Rossion (2018) showed that this quasi-disappearance of the effect after 3 s in the present paradigm is not due to natural decay of the effect over time but is related to the introduction of a new face identity during the alternation sequence (the identity alternated with the adapted identity). As a matter of fact, due to the relatively fast rate of stimulation, the new identity is also repeated many times during the sequence so that neural adaptation to the novel face can rapidly reduce the asymmetrical neural response between the two identities.

## Conclusions

In summary, we provide a highly sensitive technique to implicitly and objectively (i.e., at a pre-defined frequency) measure an individual's ability to generalize identity across different natural views of familiar faces with EEG. A short adaptation period to varying natural images of a famous identity substantially increases an asymmetrical neural response between this identity and another one, reflecting participants' ability to generalize identity across different face viewing conditions. Obviously, generalization of this effect to other face stimuli deserves to be evaluated in future studies, and specific identities should be used for different cultures and individuals, as for every paradigm using (famous or personally) familiar face identities. However, considering the very short testing time required to obtain significant effects even at the individual level (i.e., 3 sequences of 45 s), without requiring explicit tasks and complex instructions, this novel FPVS-EEG adaptation paradigm may be particularly useful to measure face identity recognition impairments in various clinical populations (e.g., Prosopagnosia, Alzheimer's disease, fronto-temporal semantic dementia,...) and evaluate the developmental trajectory of this function from a very young age.

## Declaration of conflicting of interest

The authors report there are no competing interests to declare.

## Author Contributions

**Justine David:** Formal analysis, Data curation, Methodology, Investigation, Visualization, Writing – original draft, Writing – review & editing; **Laurent Koessler:** Funding acquisition, Methodology, Writing – review & editing; Supervision; **Bruno Rossion:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review & editing

## Acknowledgments

The authors would like to thank Holger Wiese and an anonymous reviewer for very helpful comments on a previous version of this manuscript.

## Funding:

This research was supported by an ERC grant (ADG HUMANFACE 101055175). JD is supported by an ANRT CIFRE grant (n°2021/0405)

## References

- Ales, J. M., & Norcia, A. M. (2009). Assessing direction-specific adaptation using the steady-state visual evoked potential: Results from EEG source imaging. *Journal of vision*, 9(7), 8-8.
- Ales, J. M., Farzin, F., Rossion, B., & Norcia, A. M. (2012). An objective method for measuring face detection thresholds using the sweep steady-state visual evoked response. *Journal of vision*, 12(10), 18-18.
- Ambrus, G. G., Kaiser, D., Cichy, R. M., & Kovács, G. (2019). The neural dynamics of familiar face recognition. *Cerebral Cortex*, 29(11), 4775-4784.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of cognitive neuroscience*, 8(6), 551-565.
- Bindemann, M., Burton, A. M., Leuthold, H., & Schweinberger, S. R. (2008). Brain potential correlates of face recognition: Geometric distortions and the N250r brain response to stimulus repetitions. *Psychophysiology*, 45(4), 535-544.
- Bruce, V. (1982). Changing faces: Visual and non-visual coding processes in face recognition. *British journal of psychology*, 73(1), 105-116.
- Bruce, V., Henderson, Z., Greenwood, K., Hancock, P. J., Burton, A. M., & Miller, P. (1999). Verification of face identities from images captured on video. *Journal of Experimental Psychology: Applied*, 5(4), 339.
- Burton, A. M., Kramer, R. S., Ritchie, K. L., & Jenkins, R. (2016). Identity from variation: Representations of faces derived from multiple instances. *Cognitive Science*, 40(1), 202-223.
- Cobb, W. A., Morton, H. B., & Ettliger, G. (1967). Cerebral potentials evoked by pattern reversal and their suppression in visual rivalry. *Nature*, 216(5120), 1123-1125.
- Davies-Thompson, J., Gouws, A., & Andrews, T. J. (2009). An image-dependent representation of familiar and unfamiliar faces in the human ventral stream. *Neuropsychologia*, 47(6), 1627-1635.
- Davies-Thompson, J., Newling, K., & Andrews, T. J. (2013). Image-invariant responses in face-selective regions do not explain the perceptual advantage for familiar face recognition. *Cerebral Cortex*, 23(2), 370-377.

Eger, E., Schweinberger, S. R., Dolan, R. J., & Henson, R. N. (2005). Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *Neuroimage*, 26(4), 1128-1139.

Ewbank, M. P., & Andrews, T. J. (2008). Differential sensitivity for viewpoint between familiar and unfamiliar faces in human visual cortex. *Neuroimage*, 40(4), 1857-1870.

Hancock, P. J., Bruce, V., & Burton, A. M. (2000). Recognition of unfamiliar faces. *Trends in cognitive sciences*, 4(9), 330-337.

Hill, H., Schyns, P. G., & Akamatsu, S. (1997). Information and viewpoint dependence in face recognition. *Cognition*, 62(2), 201-222.

Jacques, C., Rossion, B., Volfart, A., Brissart, H., Colnat-Coulbois, S., Maillard, L., & Jonas, J. (2020). The neural basis of rapid unfamiliar face individuation with human intracerebral recordings. *NeuroImage*, 221, 117174.

Jenkins, R., White, D., Van Montfort, X., & Burton, A. M. (2011). Variability in photos of the same face. *Cognition*, 121(3), 313-323.

Johnston, R. A., & Edmonds, A. J. (2009). Familiar and unfamiliar face recognition: A review. *Memory*, 17(5), 577-596.

Leopold, D. A., Rhodes, G., Mueller, K. & Jeffery, L. The dynamics of visual adaptation to faces. *Philosophical Transactions of the Royal Society of London B* 272, 897–904 (2005)

Lithfous, S., & Rossion, B. (2018). Electrophysiological individual face adaptation effects with fast periodic visual stimulation resist long interruptions in adaptation. *Biological psychology*, 133, 4-9.

Liu-Shuang, J., Ales, J., Rossion, B., & Norcia, A. M. (2015). Separable effects of inversion and contrast-reversal on face detection thresholds and response functions: A sweep VEP study. *Journal of vision*, 15(2), 11-11.

Megreya, A. M., & Burton, A. M. (2006). Unfamiliar faces are not faces: Evidence from a matching task. *Memory & cognition*, 34, 865-876.

Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottareau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. *Journal of vision*, 15(6), 4-4.

Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2005). View-independent coding of face identity in frontal and temporal cortices is modulated by familiarity: an event-related fMRI study. *Neuroimage*, 24(4), 1214-1224.

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. (2016a). Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. *Neuropsychologia*, 91, 9-28.

Retter, T. L. & Rossion, B. (2016b). Visual adaptation provides objective electrophysiological evidence of facial identity discrimination. *Cortex*, 80, 35-50

Retter, T. L. & Rossion, B. (2017). Visual adaptation reveals an objective electrophysiological measure of high-level individual face discrimination. *Scientific Reports*, 7:3269, 1-10

Retter, T. L., Jiang, F., Webster, M. A. & Rossion, B. (2018). Dissociable effects of inter-stimulus interval and presentation duration on rapid face categorization. *Vision Research*, 145, 11-20

Retter, T. L., Rossion, B., & Schiltz, C. (2021). Harmonic amplitude summation for frequency-tagging analysis. *Journal of Cognitive Neuroscience*, 33(11), 2372-2393.

Rossion, B., & Boremanse, A. (2011). Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. *Journal of Vision*, 11(2), 16-16.

Rossion, B., Torfs, K., Jacques, C., & 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(1), 18-18.

Rossion, B. & Michel, C. (2018). Normative accuracy and response time data for the computerized Benton Facial Recognition Test (BFRT-c). *Behavior Research Methods*, 50, 2442-2460

Schweinberger, S. R., Pickering, E. C., Jentsch, I., Burton, A. M., & Kaufmann, J. M. (2002). Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. *Cognitive Brain Research*, 14(3), 398-409.

Sergent, J., Ohta, S., & Macdonald, B. (1992). Functional neuroanatomy of face and object processing: a positron emission tomography study. *Brain*, 115(1), 15-36.

Spekreijse, H., Van der Tweel, L. H., & Zuidema, T. (1973). Contrast evoked potentials in man. *Vision Res*, 13, 1577-1601.

Tyler, C. W., & Kaitz, M. (1977). Movement adaptation in the visual evoked response. *Experimental Brain Research*, 27, 203-209.

Troje, N. F., & Kersten, D. (1999). dependent recognition of familiar faces. *Perception*, 28(4), 483-487.

Victor, J. D., & Zemon, V. (1985). The human visual evoked potential: Analysis of components due to elementary and complex aspects of form. *Vision Research*, 25(12), 1829-1842.

Wang, Z., Bovik, A. C., Sheikh, H. R., & Simoncelli, E. P. (2004). Image quality assessment: from error visibility to structural similarity. *IEEE transactions on image processing*, 13(4), 600-612.

Weibert, K., Harris, R. J., Mitchell, A., Byrne, H., Young, A. W., & Andrews, T. J. (2016). An image-invariant neural response to familiar faces in the human medial temporal lobe. *Cortex*, 84, 34-42.

Yan, X., Goffaux, V., & Rossion, B. (2022). Coarse-to-fine(r) automatic familiar face recognition in the human brain. *Cerebral Cortex*, 32, 1560-1573

Young, A. W., McWeeny, K. H., Hay, D. C., & Ellis, A. W. (1986). Matching familiar and unfamiliar faces on identity and expression. *Psychological research*, 48(2), 63-68.