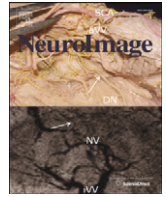




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# A steady-state visual evoked potential approach to individual face perception: Effect of inversion, contrast-reversal and temporal dynamics

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## ABSTRACT

Presentation of a face stimulus for several seconds at a periodic frequency rate leads to a right occipito-temporal evoked steady-state visual potential (SSVEP) confined to the stimulation frequency band. According to recent evidence (Rossion and Boremanse, 2011), this face-related SSVEP is largely reduced in amplitude when the exact same face is repeated at every stimulation cycle as compared to the presentation of different individual faces. Here this SSVEP individual face repetition effect was tested in 20 participants stimulated with faces at a 4 Hz rate for 84 s, in 4 conditions: faces upright or inverted, normal or contrast-reversed ( $2 \times 2$  design). To study the temporal dynamics of this effect, all stimulation sequences started with 15 s of identical faces, after which, in half of the sequences, different faces were introduced. A larger response to different than identical faces at the fundamental (4 Hz) and second harmonic (8 Hz) components was observed for upright faces over the right occipito-temporal cortex. Weaker effects were found for inverted and contrast-reversed faces, two stimulus manipulations that are known to greatly affect the perception of facial identity. Addition of the two manipulations further decreased the effect. The phase of the fundamental frequency SSVEP response was delayed for inverted and contrast-reversed faces, to the same extent as the latency delay observed at the peak of the face-sensitive N170 component observed at stimulation sequence onset. Time-course analysis of the entire sequence of stimulation showed an immediate increase of 4 Hz amplitude at the onset (16th second) of different face presentation, indicating a fast, large and frequency-specific release to individual face adaptation in the human brain. Altogether, these observations increase our understanding of the characteristics of the human steady-state face potential response and provide further support for the interest of this approach in the study of the neurofunctional mechanisms of face perception.

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## Introduction

The perception of faces by the human brain continues to be the topic of intense research in vision science and cognitive neuroscience (Calder et al., 2011). Chief among the issues to understand is how the human visual system performs rapid discrimination of different individual faces, despite their high visual similarity. This issue was addressed in a recent study (Rossion and Boremanse, 2011), in which an individual face stimulus was presented at a periodic rate (3.5 Hz) to human observers for 84 s, while recording high-density scalp electroencephalogram (EEG). Such periodic visual stimulation is known to elicit periodic responses detectable in the human EEG, known as steady-state visual evoked potentials (SSVEPs, Regan, 1966, 1989, 2009). In the study of Rossion and Boremanse (2011), a face stimulus presented at a rate of 3.5 Hz (i.e., every 285.7 ms) elicited a robust SSVEP response over the posterior electrode sites of the brain that

was confined to the narrow 3.5 Hz frequency band and its harmonics ( $2F = 7$  Hz,  $3F = 10.5$  Hz, ...). More interestingly, and directly related to the issue of understanding how individual faces are discriminated, the 3.5 Hz fundamental frequency response, and its second harmonic (7 Hz) only, were much larger when the face identity changed at every cycle than when the same face was presented throughout the stimulation sequence. This individual face repetition effect can be related to the well-known reduced neural response to repeated compared to unrepeated visual shapes that has been first reported at the neuronal level in the monkey inferior temporal (IT) cortex (e.g., Baylis and Rolls, 1987; Miller et al., 1991; Ringo, 1996), and later in humans in many neuroimaging studies (see Grill-Spector et al., 2006 for a review). Although this effect may not have the same basis when recorded at different levels of organization and with different methods (Krekelberg et al., 2006; Sawamura et al., 2006), it can be generally defined as a form of habituation, repetition suppression or visual adaptation effect (Grill-Spector et al., 2006; Henson and Rugg, 2003; Kohn, 2007).

Interestingly, the individual face repetition effect as observed for faces in SSVEP is restricted to the scalp area over the right occipito-temporal cortex (Rossion and Boremanse, 2011). This topography is typical of face-sensitive responses usually observed with other approaches, in particular with the N170 face-sensitive event-related potential (ERP) recorded to

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transient face stimulation (Bentin et al., 1996; George et al., 1996; see Eimer, 2011; Rossion and Jacques, 2008, 2011 for reviews; see also e.g., Halgren et al., 2000; Tanskanen et al., 2005; for studies in magnetoencephalography recording a similar M170 component) and with the scalp localization of the amplitude reduction of the N170 following the immediate repetition of an individual face stimulus (e.g., Jacques et al., 2007). Moreover, inverted faces also elicited robust SSVEP responses at the stimulation frequency and second harmonic, but these responses were not larger when face identity changed at every cycle than when the same face was presented. This latter observation supported the view that the SSVEP effect observed for upright faces was not due to low-level visual differences between different faces (Rossion and Boremanse, 2011).

The main interest of this initial SSVEP study of individual face perception was to show that a simple approach, whose high signal-to-noise ratio (SNR) offers many advantages (recording speed, objective identification and quantification of the response of interest, see Regan, 1989), can be fruitful to investigate the perception of individual faces under many conditions and in different populations (see Rossion and Boremanse, 2011 for a full discussion of this issue).

In the present study we aimed at strengthening and extending this approach of recording steady-state face potentials to different stimulation conditions, understanding better the dynamics of this SSVEP individual face repetition effect, and relating it more tightly to the well-known transient N170 response to faces.

In order to strengthen the SSVEP approach in comparison to the previous study we presented individual faces to a larger sample of participants (20), at upright and inverted orientation. We also obtained two recordings instead of only one for each condition from each participant to obtain even more robust data than in the previous study. However, there were other, more important, differences with respect to our previous study.

First, in the current study, faces were presented at a slightly higher rate (4 Hz) than previously used, reducing the delay between individual face stimulation to 250 ms. A shorter delay leads to a higher number of cycles recorded during the same period of time, possibly increasing SNR of the SSVEP response. Most importantly, this change should also enhance the individual face repetition effect, which is best observed in transient ERP studies with short interstimuli intervals (e.g., Jacques et al., 2007; see also Noguchi et al., 2004). Nevertheless, the visual stimulation was kept at a relatively low rate for a SSVEP study in order to take full advantage of the fact that the SSVEP is a complex-valued quantity with both amplitude and phase information. While amplitude gives information about the response gain of activated neural populations that synchronize with the frequency-tagged stimuli, phase is related to the relative delay of the responses, providing information about response timing (e.g., Appelbaum et al., 2006; Cottureau et al., 2011; Regan, 1989). However, the phase of the steady-state ERP measured at high temporal frequencies has a fundamental ambiguity: if the stimulus frequency is 10 Hz, for instance, then it is unclear whether one is measuring the response after a fraction of a response period (e.g., 70 ms), or to that fraction plus one full cycle (an additional 100 ms, e.g., 170 ms) or even two full cycles (an additional 200 ms, e.g., 270 ms). In contrast, the phase of the response at a relatively low frequency stimulation such as 4 Hz should allow the estimation of timing differences between conditions, such as the presence of a systematic delay for inverted as compared to upright faces, as typically found for the N170 (e.g., Bentin et al., 1996; Rossion et al., 1999). While there was a hint of such effects in our previous SSVEP study, we aimed to explore this more systematically here, in relationship to latency differences between upright and inverted faces observed at the N170 recorded in the same study.

A second difference from our previous study is that here grayscale instead of colored faces were used, for two reasons. First, in order to test whether the release from the individual face repetition effect could be observed without the presence of color cues that differ between

individual faces. Second, to introduce a second control condition in the study, namely contrast-reversed faces. Together with picture-plane inversion (e.g., Yin, 1969; for recent reviews see Rossion, 2008, 2009), contrast reversal is the other major manipulation that dramatically disrupts the perception of individual faces (Galper, 1970; Galper and Hochberg, 1971; for reviews see Bruce and Humphreys, 1994; Russell et al., 2006). Contrast-reversal provides a complementary control condition to the use of inverted faces. Indeed, while inversion affects primarily the perception of shape-related facial information (Jiang et al., 2011), contrast-reversal affects mainly the perception of surface cues, also called pigmentation (texture, etc., see Russell et al., 2006). Moreover, in our SSVEP paradigm, the fixation point is defined relative to the face (on the top of the nose), so that the relative amount of visual stimulation to the lower and upper visual fields changes with face orientation. However, contrast reversal does not entail a change in the position fixation, so that the amount of visual stimulation to the upper/lower visual field remains constant when comparing typical grayscale faces to contrast-reversed faces. For this reason, inversion and contrast-reversal are two manipulations that offer complementary controls to typical faces in this paradigm. A last interest of using contrast-reversed faces is that such a transformation also leads to a significant delay of the N170 (Itier and Taylor, 2002), allowing us to also test for such phase-delays in the steady-state response to faces.

Finally, we introduced an important modification in the present study, both in order to estimate better the SSVEP individual face repetition effect and to study its temporal dynamics. In the previous study (Rossion and Boremanse, 2011), two stimulation sequences that differed as early as the second stimulus onset (i.e., face AAAA... vs. face ABCD...) were compared. One limitation of this stimulation mode is that in the first condition the face identity is repeated while the SSVEP response is just beginning to emerge (i.e., while the system is becoming entrained to the stimulation frequency rate). Therefore, any putative repetition suppression effect taking place at the beginning of the sequence – as early as the first face identity repetition – might be masked by the increase of the SSVEP response. As a result, a fair assessment of the temporal dynamics of the repetition suppression effect cannot be achieved in such a paradigm. As a matter of fact, in the study of Rossion and Boremanse (2011), the repetition suppression effect for individual faces seemed to take more than 10 s to emerge. Although SSVEP amplitude appears to decrease only following the prolonged (tens of seconds) repetition of the same pattern reversal (Heinrich and Bach, 2001; Peachey et al., 1994), such a timeline is not compatible with the observation of individual face repetition effects observed as early as the second presentation of a stimulus in transient ERP studies (N170, e.g., Heisz et al., 2006; Itier and Taylor, 2002; Jacques et al., 2007; Martens et al., 2006; Vizioli et al., 2010). To take into account this issue in the present study, the two conditions of interest started with the repeated presentation of the same face for 15 s (i.e., AAA... vs. AAA...). Then, in one of the two conditions, different face identities were presented until the end of the stimulation sequence (i.e., AAA...BCD...), while in the other condition, the face identity remained the same (i.e., AAA...AAA...). Individual face repetition effects were assessed by comparing amplitude at the fundamental and second harmonics of the two conditions *after* the 16th second, but also by considering the dynamics of the changes in the SSVEP response at the 16th second onset corresponding to a first face identity change.

## Materials and methods

### Participants

Twenty healthy adult participants (all right-handed, age range 18 to 26, 7 males) with normal or corrected-to-normal vision took part in the SSVEP study for payment. Written informed consent was obtained from all participants prior to the experiment.

## Stimuli

Thirty-six (18 males) grayscale face stimuli from the Tubingen Max Planck Institute (MPI) database of laser-scanned (Cyberware TM) heads were used in this study. They were cropped for external features (hair and ears) but their overall shape was preserved. All face stimuli were unfamiliar to the participants. The size of the basic set of faces was  $4^\circ \times 5.73^\circ$  of visual angle, but the face size increased or decreased at each presentation (see the [Procedure](#) section below). All face stimuli were equalized in luminance within each set. The stimuli were not matched in contrast within each set because the face stimuli were taken under the same conditions, and some faces are more contrasted (e.g., faces with dark hair and eyebrows) than others, a cue that is diagnostic to individualize faces. They were presented under 4 different conditions: upright grayscale faces, inverted (vertically flipped) grayscale, upright contrast-reversed and inverted contrast reversed. Note that the contrast variations within a set of faces are preserved by the two manipulations, contrast reversal and inversion, so that this factor is controlled in the paradigm.

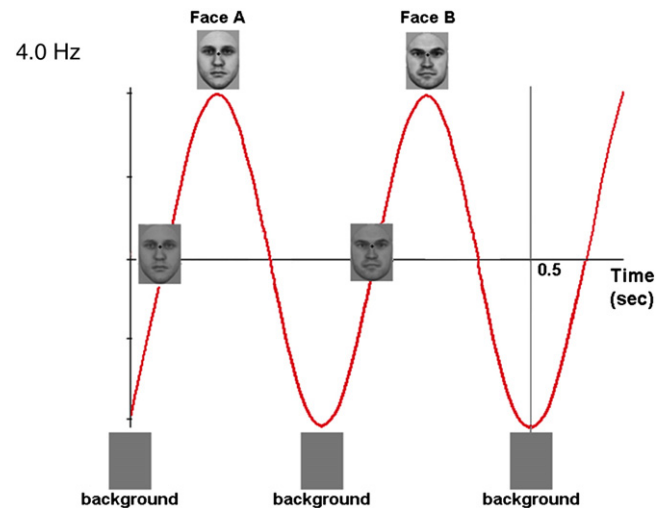
## Procedure

After electrode-cap placement, participants were seated in a light- and sound-attenuated room, at a viewing distance of 100 cm from the computer monitor. Stimuli were displayed using a custom-made application running on Matlab (The Mathworks), on a light gray background. The stimulation was as follows. In each condition, a face stimulus appeared and disappeared (contrast modulation) on the screen, at a stimulation rate of 4 faces/s (one face every 250 ms, with 8 changes/s when considering both face onset and offset). The stimulation function was sinusoidal (sinusoidal contrast-modulation) ([Fig. 1](#)). Thus, following the beginning of the stimulation sequence (background), each pixel reaches the full luminance value of the face stimulus after half a cycle ( $250 \text{ ms} / 2 = 125 \text{ ms}$ ). We used a sinusoidal contrast-modulation function, as the original study of [Regan \(1966\)](#) and in several previous studies with low-level visual stimuli ([Victor and Conte, 2000](#); [Di Russo and Spinelli, 2002](#); [Sutoyo and Srinivasan, 2009](#); [Zemon and Ratliff, 1984](#); see also [Giani et al., 2012](#), for a sinusoidal modulation of luminance and size) and our own previous investigation with faces ([Rossion and Boremanse, 2011](#)). One practical advantage of this mode of stimulation is that it is a smoother stimulation mode than a square wave stimulation, a parameter that makes the experiment more comfortable for the participant. This factor is especially important given the long stimulation duration used here.

A trigger was sent from the parallel port of the stimulation computer to the EEG recording computer at the beginning of the sequence, and at each minimal level of visual stimulation (gray background maxima, [Fig. 1](#)).

There were two kinds of stimulation sequences for each of the 4 conditions.

In the *identical face* condition, the same face picture, chosen randomly for each stimulation sequence in each set of faces, was presented during the whole stimulation duration (84 s). In the *different face* condition, the same face identity was presented for the first 15 s, and from then on the face identity changed with every cycle until the end of the sequence. In that condition, 18 individual faces of the same sex were used and presented in random order in the sequence. The same face identity never appeared twice subsequently, so that the face identity change rate was always 4 Hz. Note that, as in [Boremanse and Rossion \(2011\)](#), in the *identical face* condition, the exact same picture was used rather than different pictures of the same person. This procedure was used first for practical reasons (i.e., difficulty of presenting 18 different pictures of the same person in the same view without introducing other factors such as expression changes) and second because in our previous face adaptation studies using transient ERPs



**Fig. 1.** The basic stimulation mode used in this study. Faces were sinusoidally contrast-modulated at a rate of 4 Hz (4 faces/s) for a sequence of 84 s (336 faces presented). The 4 Hz rate means that it takes half a cycle (125 ms) for the first face to be fully visible, even though a face stimulus can be detected with less contrast (here the faces at intermediate levels of contrast are also displayed). Face size changed randomly at every cycle. The basic manipulation is between a condition in which the face presented with each cycle differs in identity from the previous faces ('different face' condition, as illustrated here) and a condition in which the exact same face appears at each cycle for the entirety of the sequence.

(N170), identical results were obtained regardless of whether different photographs of the same person ([Jacques et al., 2007](#)), or the exact same photograph (e.g., [Caharel et al., 2009b](#); [Jacques and Rossion, 2009](#); [Kuefner et al., 2010](#)) were used as the adapter and target faces. Nevertheless, to minimize low-level (i.e., pixelwise) adaptation, the face stimulus changed substantially in size with each presentation, i.e. at a rate of 4 Hz, in all conditions (random face size between 82% and 118% of base face size, so that the maximal increase or decrease of size between two cycles can be of 44%:  $118 - 82 / 82$ ). As in our previous study ([Rossion and Boremanse, 2011](#)), a long stimulation duration was used, for two reasons. First, as explained above, the repetition suppression effect for individual faces seems to take more than 10 s to emerge ([Rossion and Boremanse, 2001](#); [Fig. 10](#)) so that a long stimulation window appears to be needed to fully characterize the temporal dynamics of the effect. Second, most importantly, with a long stimulation window, one can apply the Fourier transform to a long recording window, so that the frequency resolution of the spectrum is very high. It means that all of the response of interest, and thus all the potential difference between conditions, can be concentrated in a discrete frequency band around the stimulation frequency. This frequency band occupies a very small fraction of the total EEG bandwidth. In contrast, biological noise is distributed throughout the EEG spectrum, resulting in a SNR in the bandwidth of interest that can be very high ([Regan, 1989](#)). Note that such long duration windows have been used in a number of previous SSVEP studies (e.g., [Chen et al., 2003](#); [Di Russo and Spinelli, 2002](#); [Giani et al., 2012](#); [Sutoyo and Srinivasan, 2009](#); [Zemon and Ratliff, 1984](#)).

Each participant performed 16 stimulation sequences of 84 s in total: 2 (identity change: identical or different faces)  $\times$  4 (types of face stimuli: upright/inverted  $\times$  grayscale/contrast reversed)  $\times$  2 repetitions (one with male faces, one with female faces). With pauses included, the whole experiment lasted about 40 min in addition to electrode cap placement.

The order of conditions was pseudo-randomized. The starting stimulation sequence was selected randomly for a given participant. The next sequence used the same type of face, but in the other face identity repetition condition. This way, sequences of the 2 conditions (different and identical faces) at a given frequency were always



presented consecutively, in alternating order. For instance, participant 1 started with a block of different contrast-reversed male faces followed by a block of identical contrast-reversed faces at 4 Hz. After 8 sequences were presented, the conditions were presented in the opposite order for the next 8 sequences (repetition). Therefore, sequences of the two critical conditions to compare (identical vs. different faces) always appeared next to each other during the course of the experiment and their order was fully counterbalanced.

During each 84 s run, the participant was instructed to fixate a small black cross located centrally on the face, slightly below the bridge of the nose (Fig. 1, see also Supplemental material S1 of Rossion and Boremanse, 2011). This fixation location corresponds roughly to the typical point for fast face identification (Hsiao and Cottrell, 2008; Orban de Xivry et al., 2008). The fixation cross changed color (black to red) briefly (200 ms) 6 to 8 times during each run and the participant was instructed to report the color changes by pressing a response key. Very few targets were missed (participants' performance between 96%–100%). Given that the SSVEP response is highly sensitive to visual attention fluctuations (e.g., Morgan et al., 1996; Müller et al., 2006), including attention to aspects of faces (Hajcak et al., in press) this orthogonal task was used to ensure that each participant maintained a constant level of attention while keeping the task difficulty constant between conditions.

#### EEG recording

EEG was recorded from 128 Ag/AgCl electrodes mounted in an electrode cap (Waveguard, ANT; for a 2D mapping of electrode labels and positions, see <http://www.ant-neuro.com/products/caps/waveguard/layouts/128/>). Electrode positions included the standard 10–20 system locations and additional intermediate positions. Vertical and horizontal eye movements were monitored using four additional electrodes placed on the outer canthus of each eye and in the inferior and superior areas of the right orbit. During EEG recording, all electrodes were referenced to AFz, and electrode impedances were kept below 10 k $\Omega$ . EEG was digitalized at a 1000 Hz sampling rate and a digital anti-aliasing filter of  $0.27 \times \text{sampling rate}$  was applied at recording (at 1000 Hz sampling rate, the usable bandwidth is from 0 to ~270 Hz).

#### EEG analysis

All EEG processing steps were carried out using BV Analyzer 2 (Brain Products, Germany), Letswave (<http://nocions.webnode.com/letswave/>) (Mouraux and Iannetti, 2008), and Matlab 7.8 (The Mathworks). For each individual participant, each EEG data recording ( $N=16$ ), including 2 s of EEG data before and after stimulus presentation, was first bandpass filtered between 0.1 and 100 Hz (Butterworth filter with a slope of 24 dB/oct). Next, electrodes with artifacts other than eyeblinks were pooled using a linear interpolation using neighboring channels. Finally, all channels were re-referenced to a common average reference (without M1/M2 channels, which picked up a lot of noise in many recordings). Then, different types of analyses were carried out.

**Frequency-domain analysis.** The first 17 s of the EEG recordings was removed. This duration corresponds to the beginning of the stimulation (15 s) in which the exact same stimulation was presented to the two conditions (identical face repeated), and two additional seconds of recording. These 2 additional seconds were excluded to avoid including any potential transient EP component that could have been elicited by the sudden change of facial identity at the 16th second onset in the condition 'different faces'. Fifty seconds of stimulation from this 18th second onset point (i.e., 18 s onset to 67 s offset) was considered for analysis. The end of the sequence was not considered because eyeblinks were more frequent toward the end of the recording, and also because a time-window of 50 s (exactly 200 cycles at 4 Hz) gives rise to a high and convenient spectral resolution of  $1/50 = 0.02$  Hz. Discrete Fourier Transform (DFT, Matlab 7.8) was applied to the resulting individual windows, and EEG amplitude (and phase) extracted at a resolution of

$1/50 = 0.02$  Hz. Signal-to-noise ratio (SNR) was computed at each channel for all frequency bins between 0 and 100 Hz as the ratio of the amplitude at the frequency of interest to the average amplitude of the 20 neighboring bins (e.g., Srinivasan et al., 1999; Rossion and Boremanse, 2011), skipping only the closest neighboring bin at each side. Averages of the amplitudes and SNR data files of each condition were made separately for each individual participant, and then grand-averaged.

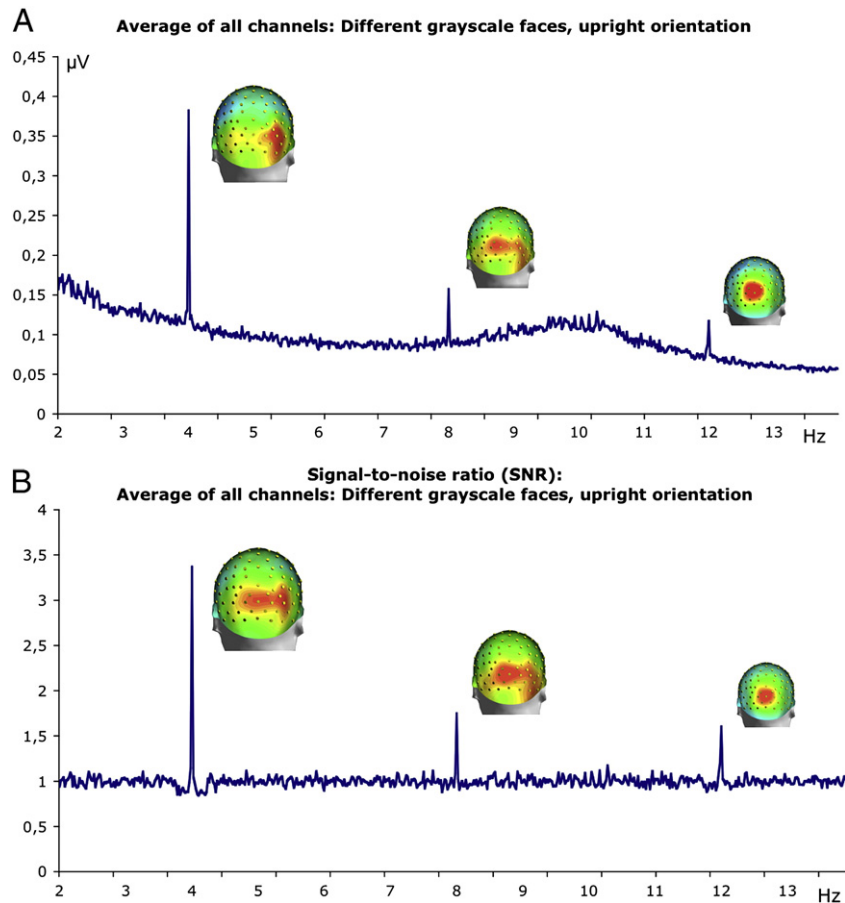
**Time domain analysis.** In order to further understand the face identity adaptation effect and the differences between upright and inverted/contrast-reversed faces, the full EEG segments (–2000 ms to 86,000 ms, i.e. 2000 ms post stimulation onset) were analyzed in the time domain or time-frequency domain. First, eyeblinks were removed in individual participants using a probabilistic Independent Component Analysis (P-ICA) as implemented in Letswave (Liang et al., 2010). Then, trials were resegmented to 50 s (17–67 s) and cut into 50 consecutive epochs of 1000 ms. These epochs were averaged for each condition and each participant separately and bandpass FFT filtered around the fundamental frequency of interest (3–5 Hz bandpass filter, width 0.3 Hz). In order to display the first ERP responses, with a particular interest for the N170 component, ICA-corrected EEG data was low-pass filtered (20 Hz FFT filter, width = 1 Hz) and epochs from the beginning of the sequence (–200 ms to 800 ms) were extracted for each trial and participant separately. Grand averages of the 4 trials of each stimulus type across the 20 participants were computed to display the ERP components to stimulation onset. Finally, the temporal dynamics of the individual face repetition effect were studied by considering both the narrow-band filtered (3–5 Hz) and the 20 Hz low-pass filtered grand-averaged responses separately for each condition surrounding the time of a novel face identity change in half of the condition (second 16th). A *time-frequency* representation based on the continuous Morlet wavelet transform (CWT) over the whole stimulation sequence (1 to 30 Hz in 100 steps of 0.3 Hz) was also computed (Mouraux and Iannetti, 2008). The Morlet wavelet consists in a complex exponential function localized in time by a Gaussian envelope. The initial spread of the Gaussian wavelet ( $\sigma$ ) was set to  $2.5/\pi\omega_0$  ( $\omega_0$ , the central frequency of the wavelet, = 20).

## Results

#### The individual face repetition effect

In all conditions, large responses confined to narrow frequency bands (0.02 Hz) of the fundamental frequency (4 Hz) and its harmonics (8 Hz, 12 Hz, ...) were observed over the whole scalp, but mainly at the back of the head, on occipital, parietal and temporal channels. Responses up to the 7th harmonic (28 Hz) were distinctly observed ( $\text{SNR} > 1$ ) on some channels, although the bulk of the response was observed at the fundamental (4 Hz) and second harmonic (8 Hz) components. Fig. 2a shows the grand-average frequency spectrum across all channels. Considering first the typical face stimulation (upright normal contrast faces) for different face identities, the fundamental frequency response peaked maximally on lateral occipital sites, with a clear right hemispheric dominance. The second harmonic also showed the right occipito-lateral, or occipito-temporal, maxima, with large responses also observed at occipital medial sites (around OZ). In contrast, from the third harmonic on, the response peaked clearly at occipital medial sites, with no evidence of a distinct response over right (or left) lateral occipital sites. Transformation of the EEG in SNR values "flattened" the spectrum and largely confirmed the distinct peaks observed at 1 F (4 Hz), 2 F (8 Hz), etc. (Fig. 2b).

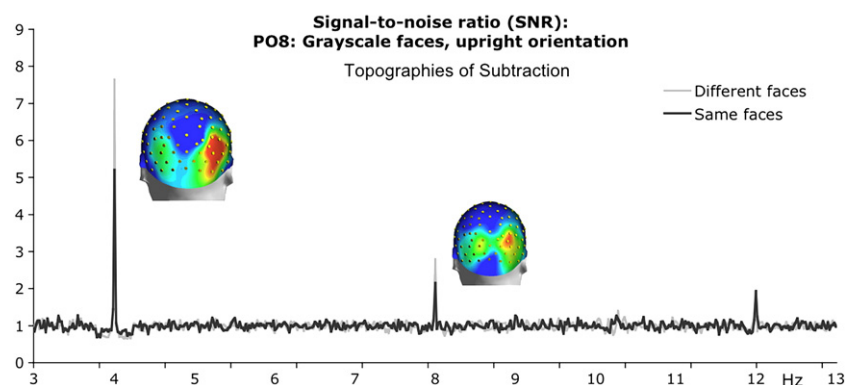
Replicating previous observations obtained at a slightly slower stimulation rate (Rossion and Boremanse, 2011), SNR was much higher when different individual faces were presented than when the exact same face was repeated for the entirety of the sequence. Importantly, this difference was not widespread but rather specific. First, it was specific to the narrow fundamental frequency band corresponding to



**Fig. 2.** A. EEG spectrum (voltage amplitude in  $\mu V$ , displayed between 2 and 14 Hz) over the entire scalp (average of all channels) for the upright grayscale face condition ('different' faces). The spectral data show the large and specific responses recorded at the fundamental face stimulation rate (4 Hz), second (8 Hz) and third (12 Hz) harmonics. The topography of the response was clearly lateralized at 4 Hz, with a right hemisphere dominance as typically observed for face stimulation. The response at the second harmonic also showed this right lateral topography. It was no longer present at the third (12 Hz) and subsequent harmonics, for which the response covered the occipital pole (centered on Oz). B. Signal-to-noise ratio spectrum (SNR, displayed between 2 and 14 Hz) over the entire scalp (average of all channels) for the upright grayscale face condition ('different' faces), and corresponding topographical maps. SNR is a form of normalization for variations of EEG amplitude. It is computed over the whole EEG spectrum by dividing EEG amplitude at the frequency bin of interest (4 Hz at a spectral resolution of 0.02 Hz, 3.99–4.01 Hz) by the average of the 20 neighboring bins (see e.g., [Chen et al., 2003](#); [Rossion and Boremanse, 2011](#)). An SNR = 1 means that there is no difference between EEG amplitude at a given bin and its neighboring bins. Note that if one considers only the most sensitive channels (around PO8), SNR reaches higher values at 4 Hz and 8 Hz than displayed here. Again, the topography of the response was clearly lateralized at 4 Hz, with a right hemisphere advantage. The response at the second harmonic also showed this right lateralized topography, and included a large response to the lowest right occipito-temporal channels. This lateralization was no longer present at the third (12 Hz) and subsequent harmonics, for which the response covered the occipital pole (centered on Oz).

the face stimulation (4 Hz) and to its second harmonic (8 Hz) ([Fig. 3](#)). Second, this larger response to different faces, compared to the identical face condition, was restricted to lateral occipital sites, with a strong right

hemispheric dominance. There was no hint of a difference at other frequencies, at the third harmonic (12 Hz, [Fig. 3](#)) or at any subsequent harmonic responses.



**Fig. 3.** Signal-to-noise ratio spectrum (SNR, displayed between 3 and 13 Hz) at electrode PO8 for upright grayscale faces. SNR was much larger when different faces rather than the exact same face were presented at each stimulation cycle, but specifically at the exact 4 Hz (fundamental frequency) and 8 Hz (second harmonic) frequency bins. The SNR peak at 12 Hz was also equally large for the 2 conditions. The topographical maps represent the difference in SNR values between the two conditions. For both the fundamental and second harmonics, the largest difference was observed over lateral electrode sites, with a right hemisphere advantage.

Considering upright grayscale faces only, we first tested for differences between the SNR values of the two conditions ('different' and 'identical' face) at all channels (124 without ocular and mastoid channels), averaging the fundamental and the second harmonic responses. A very clear pattern emerged, with only 8 contiguous right occipito-temporal channels surviving a very conservative Bonferroni correction (Fig. 4). A few other channels were significant at lower statistical thresholds ( $p < 0.005$ ;  $p < 0.01$ ), and these channels were all localized around that right occipito-temporal region, or formed a contiguous region on left prefrontal sites, with one channel disclosed on the left homologous occipito-temporal region (P7, Fig. 4). At a more liberal  $p < .05$  threshold, there were a few additional significant channels over these 3 regions on the scalp, including a region of 6 contiguous channels on left occipito-temporal sites (CPP5h, P5, P7, PO7, PPO9h, PO9). Even at a  $p < 0.05$  threshold, there were no channels associated with a significantly larger response when the same face was presented than when different faces were presented. Analyses of EEG amplitudes rather than SNR values gave essentially the same results.

In summary, with more data (20 participants instead of 12, 2 repetitions instead of one by participant/condition) and the slightly higher stimulation frequency rate of the present study compared to our previous study (Rossion and Boremanse, 2011), we largely replicated previous observations of a SSVEP individual face repetition effect primarily observed over the right occipito-temporal region.

#### Effects of inversion and contrast-reversal

Based on this analysis but also more generally on our previous study and the typical topography of the N170 face-sensitive response, we defined a region of interest (ROI) on right occipito-temporal sites by considering the 8 contiguous channels, and pooled the SNR values at these channels. SNR values of this ROI, averaged over 4 Hz and 8 Hz (see Figs. 4–6), were entered into a repeated measure analysis of variance (ANOVA) with *identity repetition* (2 levels: "different vs.

'identical'), *orientation* (2: upright vs. inverted), and *contrast* (2: grayscale vs. contrast-reversed) as within subject factors.

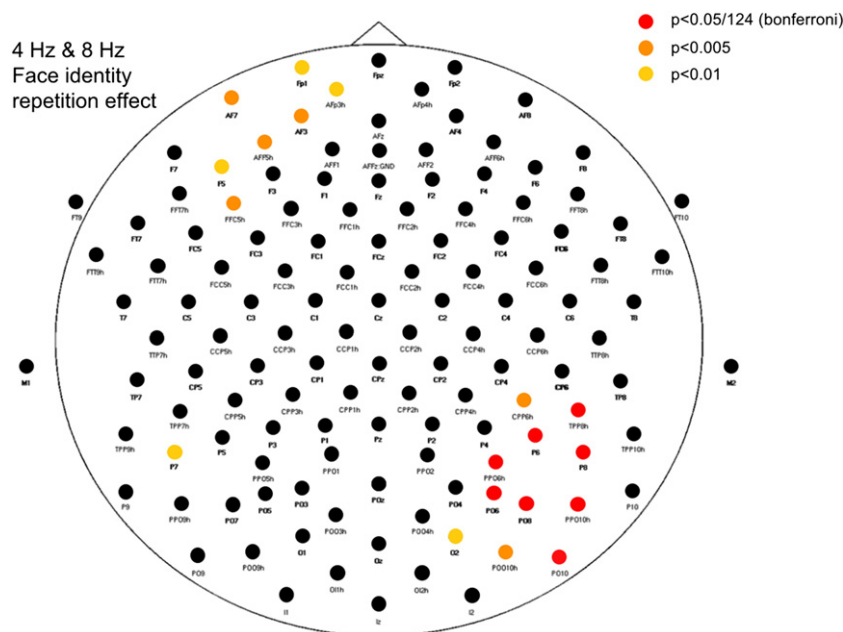
There was a highly significant main effect of *identity repetition* ( $F_{1,19} = 27.76$ ;  $p < 0.0001$ ), due to the large decrease of amplitude when the same face was presented repeatedly as compared to the presentation of different face identities. However, this effect was qualified by two two-way interactions (*contrast* × *identity repetition*:  $F_{1,19} = 12.29$ ;  $p < 0.0024$ ; *identity repetition* × *orientation*:  $F_{1,19} = 4.95$ ;  $p < 0.038$ ). All other comparisons were non-significant ( $ps > 0.1$ ). There were larger responses to different than identical faces for all face formats (post-hoc tests, all  $ps < .01$ ), except for contrast reversed inverted faces ( $p = 0.54$ ). The interactions were due to a larger individual face repetition effect for upright as compared to inverted faces, and for grayscale as compared to contrast-reversed faces (Fig. 5).

We also ran a complementary analysis on the left hemisphere ROI (homologous channels pooled), for which there was only a main effect of *contrast* ( $F_{1,19} = 10.54$ ;  $p < 0.0042$ ; grayscale > contrast-reversed), and a two way interaction between *orientation* and *contrast* ( $F_{1,19} = 7.34$ ;  $p < 0.014$ ). The only interaction involving the factor *identity repetition* was between *identity repetition* and *contrast* ( $F_{1,19} = 9.21$ ;  $p < 0.022$ ), and reflected a larger face identity repetition suppression effect for grayscale as compared to contrast-reversed faces.

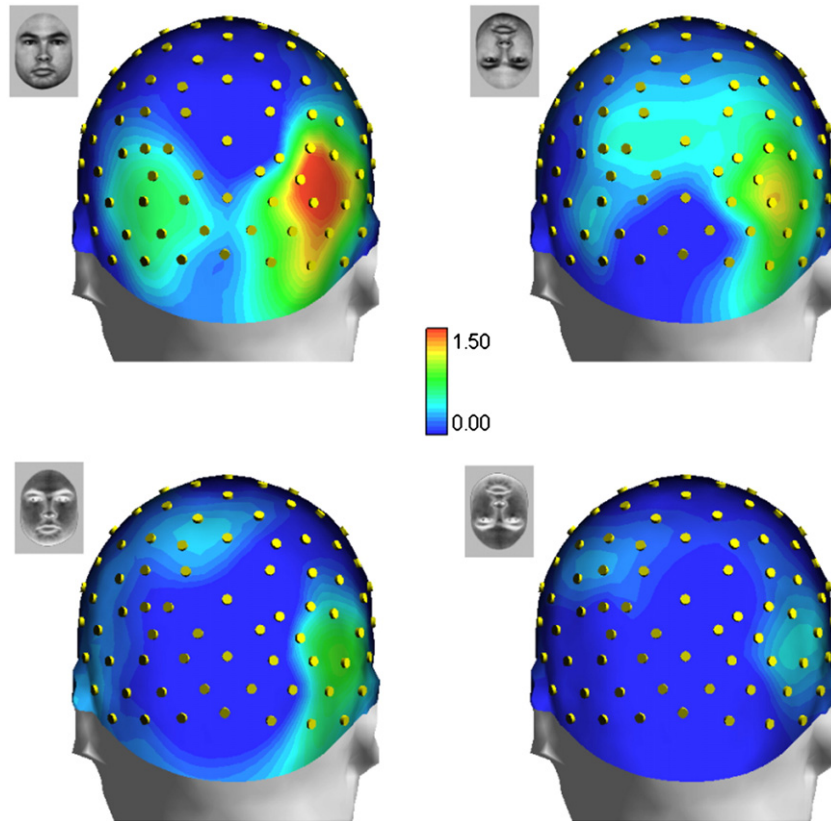
Although the first and second harmonics presented the same response profile for upright grayscale faces, we also conducted separate analyses for each response, considering all conditions.

#### Fundamental (4 Hz) response

For the 4 Hz response in the right hemisphere, there was a main effect of *identity repetition* ( $F_{1,19} = 34.38$ ;  $p < 0.0001$ ), which was qualified by a *contrast* × *identity repetition* interaction ( $F_{1,19} = 12.25$ ;  $p < 0.0024$ ), and a marginally significant three-way interaction between *contrast*, *identity repetition* and *orientation* ( $F_{1,19} = 3.75$ ;  $p < 0.068$ ). This interaction effect reflected the smaller face identity repetition effect for inverted contrast-reversed faces than both upright ( $p = .004$ ) and inverted grayscale faces



**Fig. 4.** Electrodes showing a significant identity-repetition effect ('different faces' > 'identical face', simple *t*-test, one-tailed on SNR values) at 4 Hz and 8 Hz for upright grayscale faces. Even if an extremely conservative Bonferroni correction for multiple tests is applied ( $p < 0.000403$ ), a number of contiguous channels at right occipito-temporal sites show a significantly larger response for different faces than when the exact same face identity is presented. Note the second cluster of significant channels located on left prefrontal sites, suggesting a dipolar activity. Interestingly, the face identity repetition effect at right occipito-temporal channels (8 channels; 4 Hz and 8 Hz) was highly correlated with the effect at left prefrontal electrodes (5 channels pool: F5, FFC5h, AFF5h, AF3, AF7):  $r = 0.68$   $p < 0.009$ ; in comparison, there was no correlation between right occipito-temporal channels and a neighboring cluster of centro-parietal channels around Pz).



**Fig. 5.** Topographical maps of the SNR subtraction ('different faces'-'identical face'), reflecting the repetition suppression effect, for all 4 conditions. Data at 4 Hz and 8 Hz is averaged, showing the overall magnitude of the individual face repetition suppression effect.

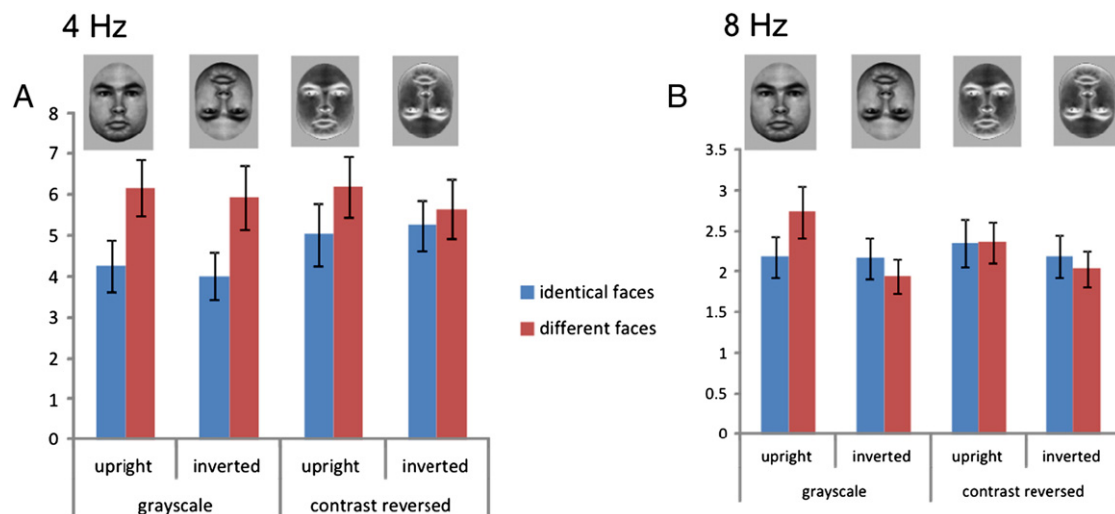
( $p = .0007$ ), but not when compared to upright contrast reversed faces ( $p = .057$ ) (Fig. 6A). All other effects were non-significant ( $ps > 0.05$ ).

In the left hemisphere, there was a main effect of *contrast* (contrast reversed > grayscale:  $F_{1,19} = 7.99$ ;  $p < 0.011$ ), a two way *orientation*  $\times$  *contrast* interaction which was marginally significant ( $F_{1,19} = 3.72$ ;  $p < 0.069$ ) and a significant two-way interaction between *identity repetition* and *contrast* ( $F_{1,19} = 7.33$ ;  $p < 0.014$ ) that reflected a larger

face identity repetition suppression effect for grayscale as compared to contrast-reversed faces.

#### Second harmonic (8 Hz) response

For the 8 Hz response, in the right hemisphere, there was a main effect of *orientation* ( $F_{1,19} = 7.60$ ;  $p < 0.013$ ), which was qualified by an *orientation*  $\times$  *identity repetition* interaction ( $F_{1,19} = 8.51$ ;  $p < 0.0088$ ),



**Fig. 6.** A. SNR for all 8 conditions (2 orientations  $\times$  2 contrast-level  $\times$  2 face identity repetition) at 4 Hz and at 8 Hz. SNR values are averaged over 8 contiguous channels on right occipito-temporal sites: PO8, PPO10h, PPO6h, P6, P8, PO10, PO6, TPP8h (Fig. 6 for 2D display of electrodes). Note that at 4 Hz, there was a large repetition suppression effect both for upright and inverted grayscale faces, with smaller effects for contrast-reversed faces. B. However, at the second harmonic (on the right), the effect was specific to the upright grayscale faces.



and a three-way interaction between *contrast* × *identity* × *repetition* × *orientation* ( $F_{1,19} = 4.69$ ;  $p < 0.043$ ). The three-way interaction was due to an increase of SNR for different faces only in the grayscale upright condition (Fig. 6B) (post-hoc:  $p < 0.004$ ; all other comparisons: NS,  $ps > .01$ ). For the left hemisphere, there was only a main effect of *contrast* (contrast reversed > grayscale:  $F_{1,19} = 4.83$ ;  $p < 0.04$ ).

In summary, we observed a very large individual face repetition effect that, nevertheless, was specific to (1) the narrow frequency bands of stimulation (4 Hz and 8 Hz) and (2) the right occipito-temporal channels. A weaker effect was also observed at left prefrontal channels with a phase-reversal of the response, suggesting a dipolar projection of the effect observed at posterior sites (Figs. 4 and 7). Contrary to our expectations, we also found a substantial individual face repetition effect for inverted faces in the present study, but only at the 4 Hz fundamental response. A reduced individual face repetition effect was also observed for contrast reversed faces, and the two manipulations, inversion and contrast-reversal, had additive effects on the individual face repetition effect. Importantly, the differences between these conditions were present only when considering the interaction with the face identity repetition factor. Hence, there was no absolute difference in SSVEP amplitude for upright/inverted and contrast-reversed faces. Finally, both for the 4 Hz and 8 Hz responses, we also tested for any difference in SNR before the onset of the change in face identity (16th second) by considering a baseline period of 5 s (10–15 s). Grouping all face formats together, there were no differences between the baselines of the 'different' and 'same' face conditions, neither for 4 Hz (right hemisphere:  $t_{19} = 1.61$ ,  $p = 0.12$ , left hemisphere:  $t_{19} = 0.82$ ,  $p = 0.42$ ), nor 8 Hz (right hemisphere:  $t_{19} = 0.13$ ,  $p = 0.9$ , left hemisphere:  $t_{19} = 0.092$ ,  $p = 0.93$ ). Testing separately all conditions did not lead to any significant baseline difference, even without a correction for multiple (16) tests: the closest to a significant baseline difference was for the 4 Hz response for grayscale inverted faces in the right hemisphere:  $t_{19} = 1.96$ ,  $p = 0.065$ , and it was in the opposite direction as predicted (non-significant larger response to 'same' faces than 'different' faces).

#### Time-domain analysis, phase differences between conditions and the N170

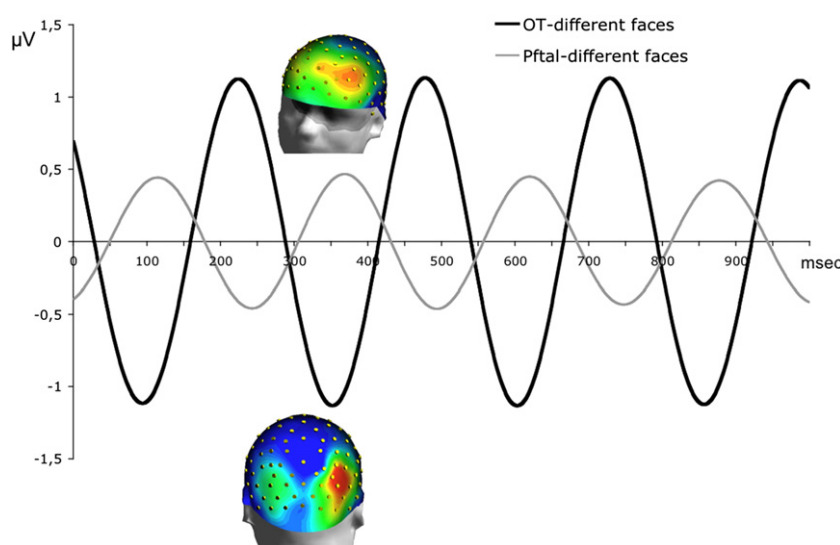
The same advantage in amplitude for different compared to identical faces was observed for bandpass-filtered data around the fundamental

stimulation frequency (3–5 Hz) (Fig. 8a), with larger effects for upright grayscale faces than inverted and contrast-reversed faces. Interestingly, the SSVEP response to inverted faces is clearly delayed with respect to the response to upright grayscale faces (Fig. 8a). A delay is also observed for contrast-reversed faces, with the maximal delay observed for inverted contrast-reversed faces (Fig. 8b). This delay seems completely independently of whether identical or different faces are presented.

The phase delay between the different face stimulus formats was examined by taking into consideration only the condition which showed a large EEG amplitude, namely when different face identities were presented. Considering a pool of the 8 right occipito-temporal channels, the phase at the fundamental frequency (4 Hz) for upright ( $29.59^\circ = 20.55$  ms, considering a 250 ms duration for a full  $360^\circ$  period) and inverted ( $-2.26^\circ = -1.57$  ms) grayscale faces was highly correlated across the 20 participants ( $r = 0.70$ ,  $p = .0006$ ). There was also a highly significant correlation between phase-values for upright grayscale and contrast-reversed faces ( $r = 0.68$ ,  $p = .0009$ ). Removing one outlier participant (#6), whose 4 Hz response was clearly out of phase and of much weaker amplitude than other participants, this correlation increased to 0.70 and 0.69 respectively (channel with maximal correlation, PO8: 0.80 and 0.75 respectively). This analysis shows that the phase of the response is variable across participants (within reasonable limits, i.e.,  $80^\circ$  or 55 ms, Fig. 9) but that differences between conditions are consistent across participants.

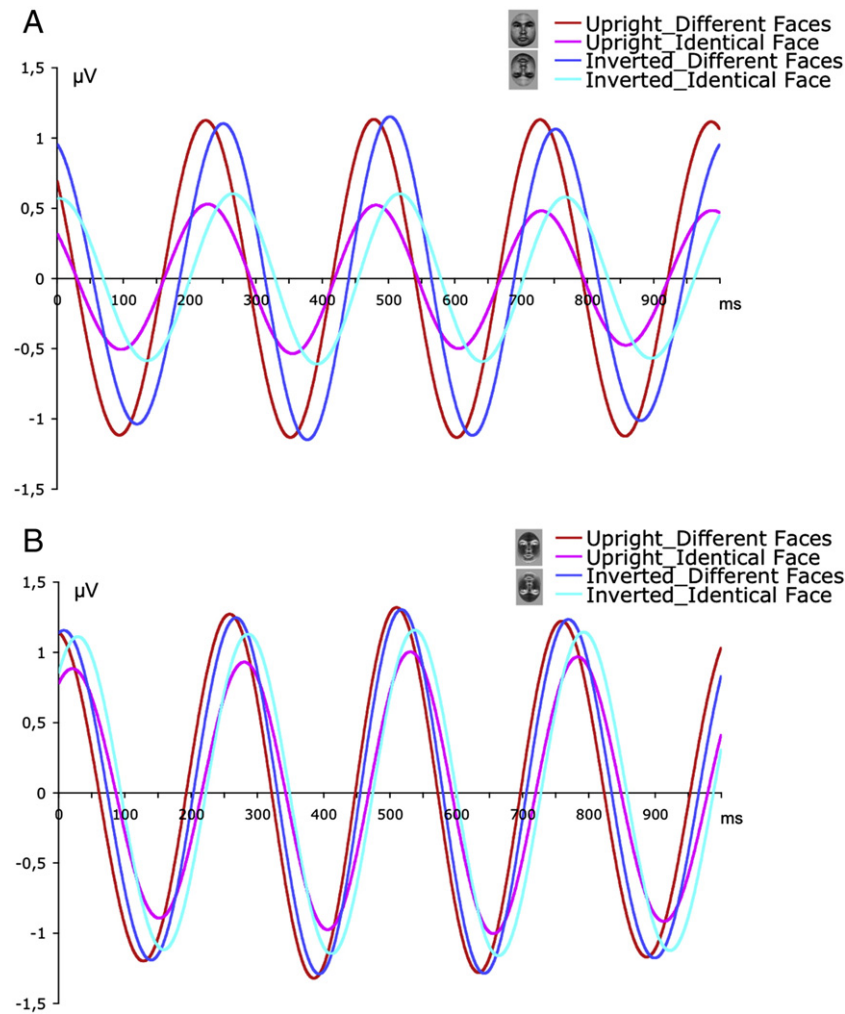
Next, we performed a repeated measure ANOVA on the phase values with *orientation* and *contrast* as factors. There was a main effect of *orientation*, inverted faces showing a significant phase-delay when compared to upright faces ( $F_{1,18} = 19.12$ ;  $p < 0.0004$ ), and a main effect of *contrast* ( $F_{1,18} = 20.6$ ;  $p < 0.0003$ ), with contrast-reversed faces also showing a delay with respect to grayscale faces (Fig. 9). There was also a significant interaction between the two factors ( $F_{1,18} = 7.82$ ;  $p < 0.012$ ), which was due to the fact that contrast-reversal delayed the phase of the SSVEP response more for upright than inverted faces (for which the response was already delayed substantially) (Fig. 9).

Converted in milliseconds, the phase-delay found for inverted faces is substantial (about 22 ms), a value that is larger than the typical latency delay observed on the N170 face-sensitive component (e.g., about 10 ms in Rossion et al., 1999). However, the stimulation mode of the present study is sinusoidal, which is different than the



**Fig. 7.** Grand-averaged epochs of 1000 ms (4 cycles), bandpass filtered (3–5 Hz), for a pool of 3 channels on right occipito-temporal electrode sites (PO8, P8, PPO10h, see Fig. 6) and on left prefrontal electrode sites (AF3, AF7, AFF3h, see Fig. 6) which show a significant face identity repetition suppression effect. Here the condition 'different faces' is displayed to show the reverse polarity between posterior and anterior electrode sites, with a larger response at posterior sites. The topographies show the difference between the 2 conditions for the combined SNR at 4 and 8 Hz (color scale as provided in Fig. 5 for posterior sites, 0–1.5 SNR, and with a maxima at 0.5 of differential SNR for the prefrontal display. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

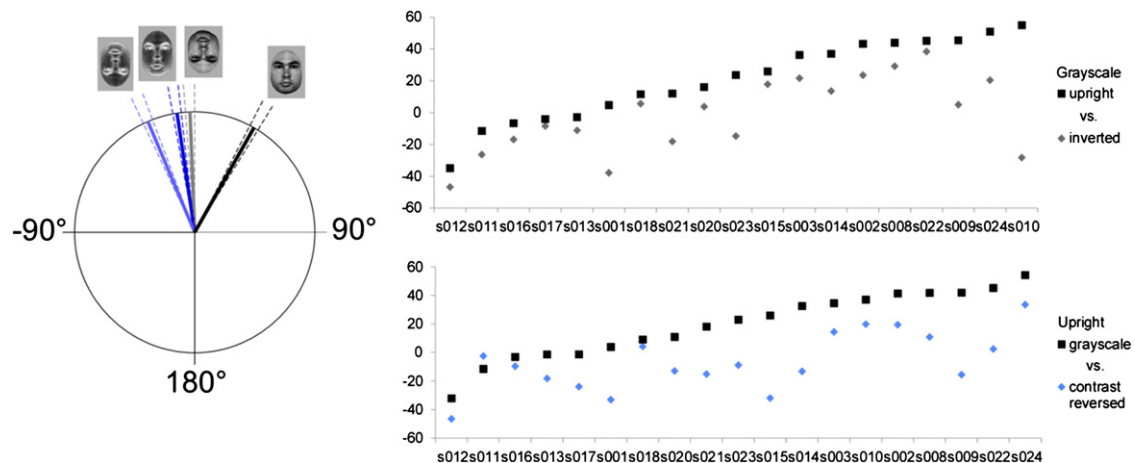




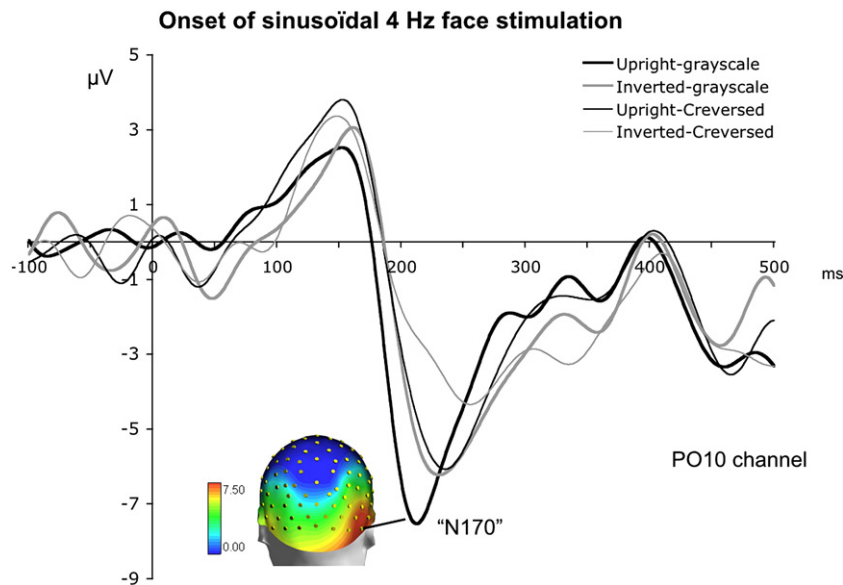
**Fig. 8.** A. Grand-averaged time-domain representation of the repetition suppression effect at 4 Hz and of the response delay between upright and inverted faces. The data of each individual participant was cropped in 50 small epochs of 1 s (4 cycles), averaged by condition and then narrow-band FFT filtered (3–5 Hz) before being grand-averaged. Here a pooling of the 3 channels (PO8, PPO10h, PO10) showing the largest responses and differences between the ‘different’ and ‘identical’ face conditions is displayed. Note the large decrease of EEG amplitude when the same face is repeated compared to when different faces are presented, and the response delay for inverted as compared to upright faces. B. Same figure as above, here for contrast-reversed faces. Repetition suppression effects are much smaller than for grayscale faces, especially for inverted faces. Although the response is already significantly delayed for contrast-reversed as compared to grayscale faces, it is further delayed by face inversion.

abrupt stimulation mode used in typical ERP studies (i.e., square wave stimulation). A fair comparison of SSVEP phase-delays can be made with the components elicited at the beginning of the stimulation

sequence in the present study, which are displayed on Fig. 10 (grand averaging, 4 trials/participant for each condition). The peak of the N170 in response to the very first face of the stimulation sequence



**Fig. 9.** Average phase components of the 19-subject (one outlier removed) SSVEP at the fundamental 4 Hz frequency (right occipito-temporal pool of electrodes). The radius of the gray circles at the end of each vector represents one standard error of the mean. Substantial phase delays (counterclockwise lags) are observed for inverted faces in comparison to upright faces, and for contrast-reversed face in comparison to grayscale upright faces.



**Fig. 10.** Grand-averaged ERPs obtained in response to the first face of the stimulation sequence at electrode PO10. This electrode was selected because it shows the largest N170 response. Only 4 trials per condition per participant are included in these ERPs. A P1-like component is recorded peaking at about 150 ms and a N170-like component at 212 ms for upright grayscale faces. These components are delayed because of the sinusoidal contrast-modulation (a full face appearing only after 125 ms) rather than the typical flash stimulation. The topographical map only shows negative values in hot colors for comparison with SNR and spectral amplitude topographies displayed in other figures. Note the largest response to upright grayscale faces compared to the other conditions rather than the typical increase of amplitude for inverted faces. This could be due either to the stimulation mode or to the fact that only the first stimulus was included in the average. Note however that the N170 shows the typical delay for inverted faces (18 ms on average here, the inverted face response peaked at 230 ms) and contrast-reversed faces, (a further delay of 5 ms) in line with the literature and with the fundamental response recorded in steady-state mode. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

was delayed by about 18 ms faces for inverted faces with respect to upright faces, and by 23 ms for contrast-reversed faces. These values correspond roughly to the phase-delay values extracted from the Fourier coefficients of the SSVEP response. Although the limited number of trials per participant prevents us from measuring a reliable N170 peak in individual participants and, consequently, from testing the correlation with SSVEP phase-delays, the similarity in the magnitude of the delay is evident. In contrast, it is worth noting that the size of the SSVEP phase delays are not at all consistent with the small latency variations between conditions observed on the early P1 component (Fig. 10).

#### *Dynamics of the individual face repetition effect*

To explore the temporal dynamics of the individual face repetition effect, we first used the continuous Morlet wavelet transform (CMT) of EEG epochs and identified stimulus-induced variations of amplitude along the whole sequence. To simplify the data display (i.e., removing all non-phase-locked frequencies), mean time-frequency (TF) windows of energy were extracted from the grand-averaged data of the participants for each condition at 8 occipito-temporal electrode sites (displayed at P08 on Fig. 11 for 0–10 Hz). This display clearly shows that the response was isolated to the narrow frequency band of stimulation for the entirety of the 84 s sequence. When identical faces were presented throughout the sequence, the magnitude of the response fluctuated over time but was clearly weaker than when different face identities were presented, for the entire duration of the sequence. Most interestingly, the difference between the two conditions starts as early as the 16th second, when different face identities were introduced in the second condition. At that time onset, the 4 Hz response appears to reach its maximum in the 'different face' condition, decreasing only slightly over time but remaining largely sustained until the end of the sequence (Fig. 11). Bandpass-pass filtering the EEG data (3–5 Hz) to focus on the fundamental stimulation frequency (4 Hz) for the length of the sequence provided congruent information with respect to the dynamics of the release from face identity adaptation (Fig. 12). It shows

that this release from adaptation immediately follows the introduction of a new face identity at the 16th second of stimulation.

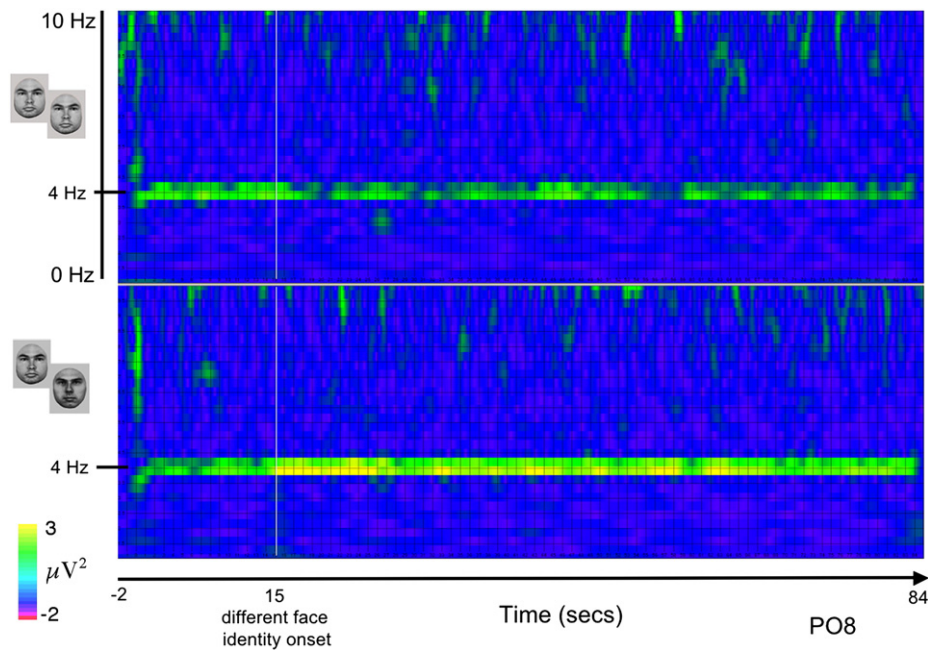
Finally, an analysis of the same data with only a 20 Hz low-pass filter shows that the onset of the different individual faces at the 16th second of stimulation leads to a large negative potential at right occipito-temporal sites (Fig. 13). This negative response, marking the detection of a change of facial identity in the sequence, has an onset latency of 250 ms and a width of 250 ms, which corresponds exactly to one cycle of stimulation at 4 Hz. Given its 250 ms width, this response does not appear to correspond to a well-known transient ERP component such as the face-related N170. Note also that although an onset of 250 ms for the detection of a change of identity seems late (compared to effects found at 160 ms in studies of transient ERPs, see Jacques et al., 2007), it is compatible with a sinusoidal contrast stimulation in which a full face is revealed only at the half cycle (125 ms).

## **Discussion**

### *Individual face repetition suppression as evidenced in SSVEP*

Presentation of upright grayscale face pictures at a fixed rate, here 4 faces/s, led to a large electrical response exactly at that specific frequency (4 Hz) and its harmonics (8 Hz, 12 Hz, ...), with a posterior distribution on the scalp covering the entire visual cortex. Replicating observations obtained with color pictures presented at a slightly lower rate (Rossion and Boremanse, 2011), both the fundamental (4 Hz) and second harmonic (8 Hz) responses were largely reduced when the exact same face was presented at every cycle compared to when different faces were presented. This larger amplitude for different as compared to identical faces was localized in narrow frequency bands corresponding to the stimulation frequency, and was observed primarily over right occipito-temporal sites.

This observation strengthens the interest of the periodic stimulation approach in EEG as a marker of the human brain's sensitivity to individual faces (Rossion and Boremanse, 2011). More generally, these findings



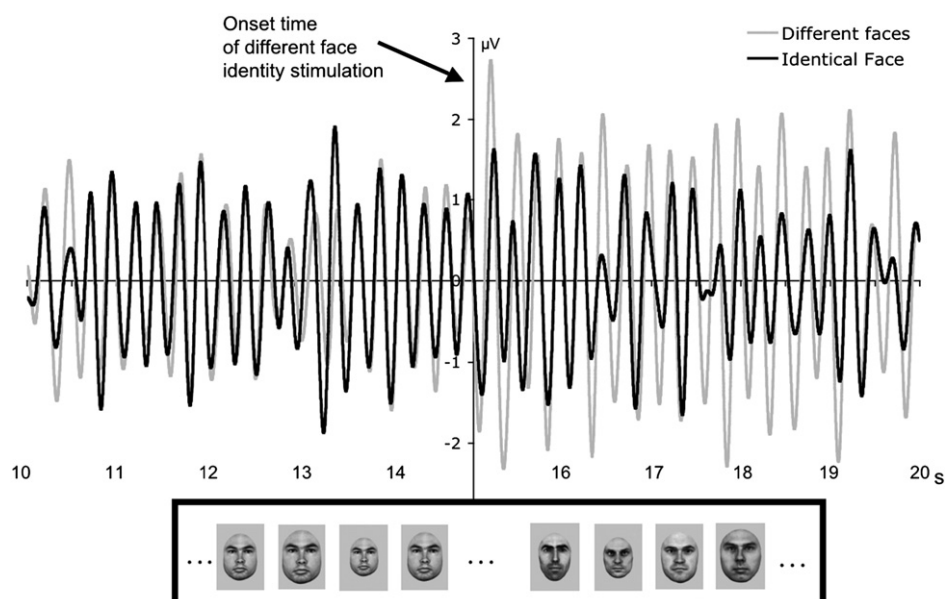
**Fig. 11.** Time-frequency analysis (Morlet wavelet) between  $-2$  and  $84$  s, displaying the data between  $0$  and  $10$  Hz in the 2 conditions of interest for upright grayscale faces. The response is centered on the  $4$  Hz stimulation band, showing a rebound and then sustained activity when different face identities are presented, as compared to when the exact same face is presented until the end of the sequence. The response at the second harmonic ( $8$  Hz) is not visible because the data was averaged across subjects in the time-domain before the FT was applied.

provide support also for electromagnetic studies that have reported a larger face-sensitive N170/M170 amplitude when different faces are presented consecutively as compared to the presentation of the same face, in particular over right occipito-temporal electrode sites (Caharel et al., 2009a, 2009b; Ewbank et al., 2008; Heisz et al., 2006; Itier and Taylor, 2002; Jacques et al., 2007; for a review see Rossion and Jacques, 2011). They also complement fMRI studies showing larger neural responses to pairs, or trains, of different faces as compared to identical faces in several face-sensitive areas of the occipito-temporal cortex with a right hemisphere dominance (e.g., Andrews and Ewbank, 2004; Gauthier et al., 2000; Gilaie-Dotan and Malach, 2007; Grill-Spector and Malach, 2001;

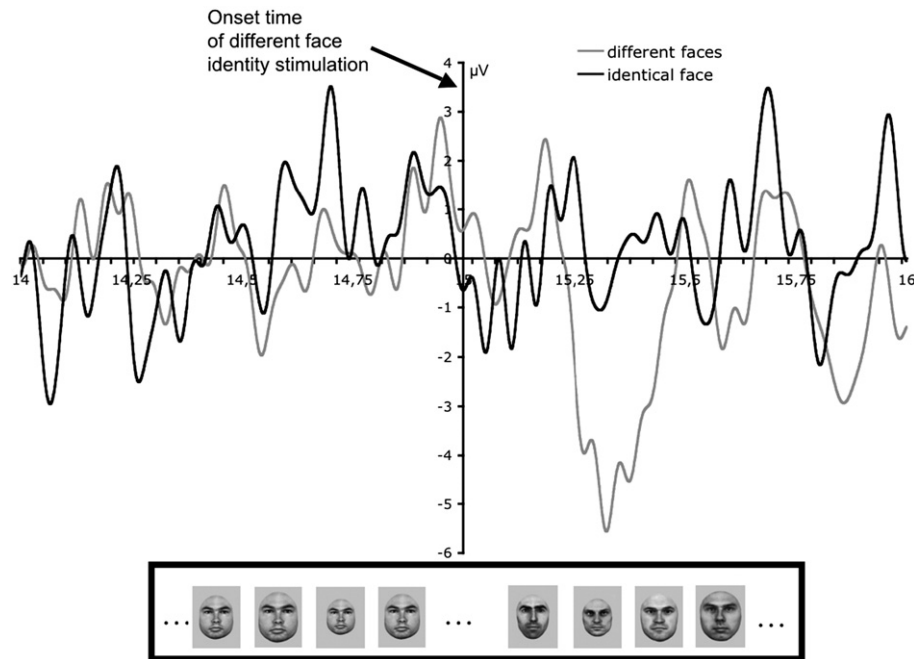
Schiltz and Rossion, 2006; Schiltz et al., 2006; Winston et al., 2004; Yovel and Kanwisher, 2005).

Interestingly, we observed another difference between the two conditions at left prefrontal electrode sites (Fig. 5). At these left prefrontal sites, the fundamental response ( $4$  Hz) was of opposite polarity to the response recorded at right occipito-temporal sites, with a slight delay. This polarity and lateralization reversal suggests a dipolar source of the effect, originating from the right occipito-temporal cortex and pointing to the left prefrontal cortex.

Overall, the present study highlights again the many advantages of the SSVEP method (Regan, 1989), supporting the idea that it can be



**Fig. 12.** Bandpass filtered EEG data centered on the fundamental stimulation frequency ( $3$ – $5$  Hz), and grand-averaged across the participants. The displayed segment (PO8 channel) shows the  $5$  s preceding the onset of a new face identity followed by different face identities at every cycle (for the 'different face' condition). There is a massive and immediate increase of amplitude in this condition relative to when the exact same face continues to be presented.



**Fig. 13.** In this figure, the data (PO8 as on Fig. 12) has been only low-pass filtered (cut-off 20 Hz) and grand-averaged, in order to show the shape of the response following the immediate introduction of the new face identity (after 15 s, or 60 faces at 4 Hz, of presentation of the exact same face). A large negative response of exactly one cycle width (about 250 ms) is elicited in this condition as compared to the condition when the stimulation remains the same.

an excellent tool to investigate the neural coding of individual faces (Rossion and Boremanse, 2011): (1) there is no ambiguity in selecting the narrow electrophysiological frequency band of interest, which is determined by the experimenter (i.e., the stimulation frequency), (2) the response of interest can easily be quantified in the different conditions, and (3) the SNR of the response of interest is quite high for a short duration experiment. Note that the advantages offered by the SSVEP approach in terms of sensitivity and objectivity are particularly present when one uses a long duration of stimulation and analysis, so that the frequency resolution of the spectrum is very high (0.02 Hz here). Since the visual system can be synchronized with extreme precision, with very little jitter between the responses to individual faces in this periodic stimulation mode, all of the response, and thus all the effect, is concentrated in a few discrete frequency bands that are very narrow and occupy a very small fraction of the total EEG bandwidth. In contrast, as mentioned in the **Materials and methods** section, biological noise is distributed throughout the EEG spectrum, resulting in a SNR in the bandwidth of interest that can be very high (Regan, 1989). Given these advantages, applying the SSVEP approach to face perception could prove extremely useful in testing the sensitivity to more subtle variations between the features which define face identity (e.g., face shape vs. surface properties, eyes or mouth, inter-distance relationships, ...) (Bruce and Young, 1998). In particular, the approach may prove invaluable for testing human populations who can be tested for only short durations and/or who present a lower SNR in their EEG data, such as infants, small children or brain-damaged patients.

#### *The effect of face inversion*

The reduced SSVEP response obtained in the 'identical face' condition cannot be accounted for by a mere effect of repetition of the low-level visual features, for several reasons. First, the effect was observed despite substantial changes of stimulus size (up to 44% if the smallest/largest face is followed by the largest/smallest face), excluding the possibility of pixel-wise repetition effects. Second, the effect was found only at the specific frequency bands of stimulation. Third, it was localized over

occipito-temporal regions, suggesting a contribution of high-level rather than low-level visual areas.

Considering the summed differential response of the system (4 Hz & 8 Hz) as reflecting its sensitivity to individual faces, there was a weaker effect for inverted as compared to upright faces. This is consistent with the observation that inversion substantially reduces discrimination and recognition for individual faces (e.g., Yin, 1969; for recent reviews see Rossion, 2008, 2009). fMRI studies have also found that face identity adaptation in the right occipito-temporal cortex may disappear with inversion (Mazard et al., 2006; Yovel and Kanwisher, 2005). Similarly, the N170 individual face repetition effect also disappears when faces are presented upside-down (Jacques et al., 2007). Yet, inverted faces can still be individualized well above chance level behaviorally, and smaller individual face repetition effects for inverted than upright faces have been observed in face-sensitive areas (Gilaie-Dotan et al., 2010; Goffaux et al., 2009). Moreover, in ERPs, individual face repetition effects for inverted faces are also found over right occipito-temporal leads – at a weaker magnitude – later than the N170 component (~210 ms, Jacques et al., 2007). Thus a reduced SSVEP individual face repetition effect for inverted faces is more consistent with the literature than an abolished effect, as previously observed (Rossion and Boremanse, 2011).

Nevertheless, the observations of the present study raise two interesting issues. First, while the effect for upright faces is highly consistent across the two studies, it is rather surprising that there was no effect at all at 3.5 Hz for inverted faces in the study of Rossion and Boremanse (2011) and a highly significant effect at 4 Hz in the present study. Preliminary observations in our laboratory with upright faces presented at multiple frequency rates suggest that if the stimulation rate is too low, that is if faces are presented with a SOA longer than 333 ms (lower than 3 Hz), then the SSVEP individual face repetition effect tends to disappear even for upright faces (Alonso Prieto and Rossion, 2011). Based on this observation, an intriguing possibility would be that a stimulation rate of 3.5 Hz – which is fast enough for the individual face repetition effect to emerge with upright faces – is too slow to provoke the same effects for inverted faces. In other words, inverted faces might need to be presented more closely in time to



each other than upright faces in order to lead to individual face repetition effects. Conversely, and this is the second issue, populations of neurons discharging at twice the rate of stimulation (8 Hz, 125 ms/cycle) might only be able to individualize faces that can be discriminated very fast, namely upright faces and not inverted faces. This would be the reason why inverted faces do not lead to individual face repetition effects at the second harmonic response here.

If these suggestions are correct, not only upright faces lead to a larger discriminative response in the human brain than inverted faces, but also their frequency-tuning function might be wider than the frequency-tuning function of inverted faces. That is, individual face repetition effects might be observed both at lower and higher frequency rates for upright than inverted faces. A complete sampling of a large number of stimulation frequencies in this paradigm, both for upright and inverted faces, will be necessary to answer this question.

### *Contrast-reversal*

A novel aspect of the present study was the extension of the paradigm to test the effects of contrast-reversed faces. As noted in the introduction, contrast-reversed faces, in which black areas are made white, light gray areas are made dark gray and so forth, are particularly difficult to recognize (Galper, 1970; Galper and Hochberg, 1971). This phenomenon, although not as well-known as the effect of picture-plane inversion, has been described and studied quite extensively not only at the behavioral level (Bruce and Langton, 1994; Hayes et al., 1986; Johnston et al., 1992; Kemp et al., 1990, 1996; Liu et al., 1999; Phillips, 1972; Russell et al., 2006; White, 2001) but also at the neural level (George et al., 1999; Itier and Taylor, 2002). Therefore, the reduced individual face repetition effect found here for contrast-reversed faces is in line with behavioral observations, and offers a useful additional control to the presentation of inverted faces: in both cases (inverted and contrast-reversed faces), the individual faces in the 'different face' conditions differ physically as much as when they are presented in the upright orientation and normal contrast. However, our face processing system cannot extract all the information efficiently for contrast-reversed and inverted faces.

Although it has been proposed that contrast-reversal affects similar cues as picture-plane inversion, namely overall shape and relative distances between features (Kemp et al., 1990; Lewis and Johnston, 1997), the evidence supporting this proposal is rather weak (Russell et al., 2006) and is inconsistent with the fact that holistic/configural processing is observed for negative faces (Hole et al., 1999; Taubert and Alais, 2011). Rather, it seems that contrast-reversal affects primarily the processing of pigmentation, or surface reflectance properties (Bruce and Langton, 1994; Liu et al., 1999; Russell et al., 2006) while inversion affects mainly shape information, not pigmentation (Jiang et al., 2011). Therefore, because both the shape and pigmentation information are important for face recognition and individualization (Jiang et al., 2006; O'Toole et al., 1999; Russell et al., 2007), it makes sense that the individual face repetition effect was reduced both for inverted and contrast-reversed faces, and to an even larger extent when the two manipulations were combined (Figs. 7 and 8).

### *The dynamics of the SSVEP (release from) adaptation effect*

In the present study, the presence of a 15 s baseline preceding the introduction of different face identities allowed us to identify with precision the dynamics of the release from the individual face repetition effect: this release takes place extremely fast, with the very first change of face identity leading to a large rebound of the electrophysiological response (Figs. 9 and 10). Interestingly, this release was largely confined to the stimulation frequency (and second harmonic), and concerned only the right occipito-temporal region. These observations point to the fast dynamics of the individual face repetition effect itself (i.e., of face identity adaptation), a hypothesis that could be tested in

future studies by inverting the presentation mode of the present study: different facial identities would be presented for 10–15 s, at which point the exact same identity would be repeated, leading to an immediate, frequency-specific, face identity adaptation effect.

### *Putative neuronal mechanisms*

What are the neuronal mechanisms of the release from face identity adaptation? In general, adaptation/habituation/repetition suppression effects observed in fMRI or EEG/MEG have been attributed at the neuronal level to either: (1) a fatigue of the neurons responding to the stimulus; (2) a sharpening of the representation, with fewer neurons being involved in coding the repeated face; or (3) a facilitation of the representation with a reduction of processing time (Grill-Spector et al., 2006). Admittedly, the effect observed here may correspond to any of these factors, or a combination of factors. However, what seems to be truly interesting here is not the mechanisms of adaptation per se but the release from adaptation due to a change of face identity. We would like to argue that this increase can only take place thanks to two characteristics of the neuronal coding of faces that are known from recordings of neurons tuned selectively to faces in the non-human primate brain (since Gross et al., 1972; see e.g., Desimone, 1991; Perrett et al., 1998). First, the release takes place because different facial identities are coded by different patterns of responses in populations of face-selective neurons (Leopold et al., 2006; Rolls and Tovee, 1995; Young and Yamane, 1992). If this were not the case, the response would continue to decrease (i.e., adapt/habituate) even when different facial identities are presented. More fundamentally, if different faces were coded by the exact same patterns of neuronal responses, then the brain would be unable to discriminate individual faces by means of face-specific mechanisms. The second characteristic is that different faces are coded within the same population of neurons (Leopold et al., 2005; Rolls and Tovee, 1995; Young and Yamane, 1992). In summary, it is the same population of neurons that code for different faces through a modulation of its patterns of response. If this were not the case, for instance if fundamentally distinct populations of neurons coded for different facial identities, then the timing and properties of the response populations would certainly be different for different faces. In such conditions, presenting different faces at every cycle could decrease rather than increase the response at a specific frequency at which the system has been entrained. If this assumption is correct, interrupting a train of identical faces by a stimulus (i.e., a nonface object) that activates a different population of neurons, with different timing characteristics (e.g., Kiani et al., 2005), should not lead to a frequency-specific increase of the EEG response, as observed here.

### *The SSVEP response is phase-delayed for inverted faces*

Compared to upright faces, the response to inverted faces was delayed by about 20 ms on average. A similar delay was observed for contrast-reversed faces, with the largest response delay again found for the faces that underwent the two transformations. This delay was roughly of the same magnitude as observed at the peak of the N170 component recorded at the onset of the stimulation (Fig. 10). As indicated in the introduction, a delayed N170 to inverted faces has been described in numerous studies (e.g., Bentin et al., 1996; Rossion et al., 1999). A N170 delay for contrast-reversed faces has also been reported (Itier and Taylor, 2002). The response delay for inverted faces is in agreement with behavioral studies showing that inverted faces are detected (Lewis and Edmonds, 2003; Rousselet et al., 2003) and individualized (e.g., Jacques et al., 2007) more slowly than upright faces. It is also compatible with delays observed for inverted faces in the mean onset latency of face-selective neurons (Perrett et al., 1988, 1998). Thus, although the absolute timing of the response is difficult to interpret (at least with a single frequency, see Regan, 1989), the systematic phase-delay of the response for inverted (and

contrast-reversed faces) shows that the SSVEP approach can be informative at least regarding the *relative* timing of face processes in the human brain. In this respect, note that the 18–20 ms delay observed here – both for the SSVEP-phase and the peak of the N170 at stimulation onset – is about two times larger than the delay usually observed on the N170 studies (e.g., Bentin et al., 1996; Rossion et al., 1999). This difference can certainly be attributed to the stimulation mode used here, in which a face is not presented abruptly (i.e., square wave stimulation) but appears progressively through a sinusoidal contrast modulation (Fig. 1). Such a sinusoidal stimulation mode, coupled with the fact that the N170 was only measured here from the few trials corresponding to the beginning of the stimulation, might also account for the fact that the N170, in the present study, was not of larger magnitude for inverted faces or contrast-reversed faces, as typically observed in ERP studies using square-wave stimulation (e.g., Rossion et al., 1999; Itier and Taylor, 2002, respectively; although see Rossion et al., 2003 for an increase of latency without amplitude effect).

#### *The steady-state face response and transient EP components: further considerations*

The phase delay observed for inverted and contrast-reversed faces, as well as the topography of the SSVEP response to the 4 Hz stimulation, may suggest that this latter response merely reflects a linear summation of many successive transient face-sensitive N170 responses. In the auditory domain for instance, it has been claimed that the 40 Hz auditory steady-state response (ASSR) can be accounted for by a superimposition of transient auditory responses to single clicks (Galambos et al., 1981; Santarelli et al., 1995). In the visual domain, attempts have been made to explain SSVEP responses to low-level stimuli (e.g., checkerboard reversal) by linear superimposition of transient event-related responses (Capilla et al., 2011; see Regan, 1989 for a discussion of this issue). However, a parallel between the N170 transient response and the face-related SSVEP recorded here must be considered cautiously for several reasons. First, while the N170 peaks at the lowest occipito-temporal electrode sites (Fig. 10, see also e.g., Fig. 3 in Caharel et al., 2009b for a N170 topography recorded with the same system and channel configuration), the topography of the fundamental and second harmonic responses recorded here were right lateralized but remained broadly distributed over the whole occipital pole (Fig. 2). This suggests that while the N170 essentially reflects the contribution of higher order visual areas, including face-sensitive areas of the occipito-temporal cortex (e.g., Deffke et al., 2007, see Rossion and Jacques, 2011 for a summary of source localization studies on the N170/M170), the SSVEP response to faces at 4 Hz certainly reflects contributions from a large set of areas, including areas that contribute to lower-level visual transient components (e.g., C1, P1) and low-level SSVEP responses (Di Russo et al., 2007; Srinivasan et al., 2006). After all, the whole SSVEP response as recorded here reflects the onset of a complex visual pattern 4 times per second, and its offset at the same rate, with changes of overall luminance and contrast at 8 Hz. There is no reason to expect that this basic SSVEP response concerns only the process reflected by the N170, which is a component reflecting essentially high-level visual processes (Rossion and Caharel, 2011). To put it differently, even if one could thoroughly predict the SSVEP response to faces via a superimposition of transient responses, it would need to be a *composite* of several transient responses (as the 40 Hz ASSR in fact, see Galambos et al., 1981), most likely including all of the responses that take place below 250 ms (one cycle at 4 Hz). A second reason to remain cautious in making parallels between the N170 and a face-related SSVEP response is that their response properties were not completely identical in the present study. For instance, as mentioned above, the N170 was larger for upright than inverted and contrast-reversed faces, which was not the case for the response at 4 Hz. Third, when introducing a new face identity in the sequence at the 16th second, we observed a large

negative response mainly at occipito-temporal sites that has a 250 ms width, that is, exactly one cycle at 4 Hz, rather than the smaller typical width of the N170, a component which is associated with power increase in the 5–15 Hz band (Rousselet et al., 2007). Therefore, the response that we observed does not appear to correspond to a well-known transient ERP component such as the N170.

Given these considerations, the relationship between the face-sensitive N170 and the face-related SSVEP response may remain a matter of debate for some time, and the resolution of this debate does not appear to be fundamental to take full advantage of the present SSVEP approach. As indicated above, the 4 Hz face-related SSVEP response and its harmonics certainly capture a wide range of low-level and high-level processes, with the 4 Hz and 8 Hz responses appearing to be generated in part by occipito-temporal regions. What is of interest in the present study is the individual face repetition effect. This effect as found here in the SSVEP has a similar topography as the effect found for faces on the N170 using a transient stimulation mode (Caharel et al., 2009b, Fig. 3), or even on later components such as the N250r (Schweinberger et al., 1995, 2002, see also Caharel et al., 2009b). Therefore, both the SSVEP and the N170 individual face repetition effects may have the same sources. However, we should not conclude that the SSVEP effect merely “reflects” the N170 effect. Rather, both measures appear to capture the same processes at a global scale, namely the discrimination of individual faces, performed by a distributed population of neurons in the occipito-temporal cortex. Contrary to transient ERP studies, the present SSVEP approach does not allow a fine-grained chronometric analysis of the time-course of these processes. Nevertheless, because the SSVEP approach carries important advantages in terms of sensitivity and objectivity, it should become a tool of choice in the study of the neuro-functional basis of face perception.

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