Temporal dynamics of repetition suppression to individual faces presented at a fast periodic rate

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ARTICLE INFO

ABSTRACT

Periodic presentation of visual stimuli leads to a robust electrophysiological response on the human scalp exactly at the periodic stimulation frequency, a response defined as a "steady-state visual evoked potential" (SSVEP, Regan, 1966). However, recent studies have shown that SSVEPs over the (right) occipito-temporal cortex are reduced when the same individual face is repeated at periodic rates of 3 to 9 Hz compared to when different faces are presented (Rossion, 2014). Here, we characterized the temporal dynamics of this repetition suppression effect. We presented different face identities at a rate of 5.88 Hz (stimulus onset asynchrony of 170 ms) for 15 s, followed by the repetition of the exact same face at this rate for 35 s. Compared to a stimulation sequence with different faces only, there was a large and specific decrease of the 5.88 Hz response when the same face was repeated at that rate. This effect was observed over the left and right occipito-temporal cortex, but not over medial occipital electrode sites where SSVEPs are typically measured. In the right hemisphere, this decrease occurred abruptly, i.e., within half a second following the introduction of the same-identity stimulation, with no further decrease until the end of the stimulation. These observations indicate that the SSVEP recorded over high-level visual areas to periodic stimulation is not steady but rather adapts immediately and fully following the repetition of the same individual face, supporting a bottom-up, stimulus-driven account of repetition suppression effects.

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1. Introduction

Two important and complementary functions of the human brain are the ability to discriminate between different visual entities, and to generalize across different presentations of the same visual entity. For instance, the human brain is able both to discriminate people by their faces rapidly and efficiently and to generalize across different viewing conditions of the same face identity. A powerful way to understand visual discrimination and generalization is by taking advantage of the phenomenon of repetition suppression (RS), i.e., the reduced (adapted) neural response to repeated compared to unrepeated visual stimuli. In particular, this effect has been reported for face stimuli at the single neuron level in the monkey inferior temporal (IT) cortex (e.g. Baylis and Rolls, 1987; Fahy et al., 1993; Li et al., 1993; Miller et al., 1991; Ringo, 1996), at the neural population level in the human ventral occipito-temporal cortex with neuroimaging (e.g. Andrews and Ewbank, 2004; Ewbank et al., 2013; Gilaie-Dotan et al., 2008; Grill-Spector and Malach, 2001; Grill-Spector et al., 2006; Henson et al., 2002) and on the human scalp with visual event-related potentials (ERPs, e.g., Eimer et al., 2011; Jacques et al., 2007; Kovács et al., 2006; Walther et al., 2013).

Although the neural mechanisms of RS are unclear, the response difference between a repeated face stimulus and face stimuli differing by a carefully controlled characteristic reveals the sensitivity of the human brain to this characteristic. This response difference occurs at a given spatio-temporal scale determined by certain factors, e.g. a single neuron, a population of neurons or a functional brain region. RS effects for faces have been observed at multiple spatial, temporal and frequency scales, both in the human and nonhuman primate brain, as indicated above (see also Gruber et al., 2004; Merzagora et al., 2014). However, since these responses are widely distributed in time, space and frequency bands, adaptation effects that arise from the comparison of repeated to unrepeated stimuli can be nonspecific (i.e. not directly related to the stimulus). Moreover, they can potentially be attributed to several factors beyond visual discrimination (attention, arousal, change detection, model adjustment, novelty detection, prediction error) (Lieder et al., 2013).

One way to circumvent this limitation is by using a periodic rate of visual stimulation eliciting a periodic brain response exactly at this stimulation rate (Adrian and Matthews, 1934). Even if the rate is fast, for instance, three or more items are presented per second, the response can be identified exactly at the frequency of stimulation by means of techniques with a high temporal resolution, such as electroencephalography (EEG)

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or magnetoencephalography (MEG). In EEG, this periodic neural response is known as the "steady-state visual evoked potential" (SSVEP, Regan, 1966, 1989; Norcia et al., 2015 for a review).

Although the SSVEP has long been thought of, and defined, as a response that is constant in amplitude and phase over time (a "steady state" response), there is recent evidence that this response is sensitive to stimulus identity repetition. Specifically, when the same visual stimulus, a given face identity, is repeated at a relatively fast periodic rate (e.g., 3.5 Hz, or a stimulus onset asynchrony of 286 ms), it leads to a reduced response compared to the presentation of different face identities exactly at that rate (Rossion and Boremanse, 2011). Importantly, this RS effect is restricted to the frequency of interest (3.5 Hz) and observed on the scalp mainly over the right occipito-temporal cortex, a scalp topography characteristic of face-sensitive responses such as the well-known N170 potential (Bentin et al., 1996; Rossion and Jacques, 2011 for review). A robust RS effect can be obtained with this approach for stimulation frequency rates of 3 to 9 Hz (Alonso-Prieto et al., 2013; Rossion and Boremanse, 2011; Rossion et al., 2012; see also Gerlicher et al., 2013; Vakli et al., 2014; see also Jonas et al., 2014 for an RS effect at 6 Hz as recorded intracerebrally in the right lateral occipital cortex).

Recording SSVEPs offers several advantages for exploring RS effects. First, the RS effect is confined to a very narrow frequency band corresponding to the stimulation frequency defined by the experimenter, so that the effect can be directly identified and quantified. Second, the SSVEP has a very high signal-to-noise ratio because the signal falls in a specific frequency band, which can be defined outside the range of frequencies associated with high levels of noise (i.e., low frequencies, alpha band). Moreover, the technique is relatively immune to artifacts (e.g. blinks, eye movements or muscular artifacts), since these artifacts spread over a wide range of frequencies while the signal is concentrated on a small stimulation frequency band (Regan, 1989; Norcia et al., 2015). This allows for robust effects to be obtained in a very short time. Third, the measure is implicit or behavior-free, since it can be obtained without performing an explicit task related to the process of interest (i.e., here, individual face discrimination, Rossion, 2014).

However, the temporal dynamics of the face identity RS effect to fast periodic stimulation remains largely unknown. Here, by "temporal dynamics", we do not mean the exact onset latency of the RS effect, which is difficult to define precisely (i.e., at the millisecond range) when a fast periodic train of stimuli is presented in a SSVEP paradigm. Rather, temporal dynamics refers here to the time taken by the periodic visual response to show suppression following the onset of stimulus repetition within a few hundreds of milliseconds, the time taken for this response to reach its minimal level, and the nature of this decay (i.e., a slow linear decrease or an abrupt decrease to its minimal level within a few hundreds of milliseconds). This issue is important to clarify in order to relate the RS effects obtained with periodic visual stimulation to other approaches and to help understand the nature of this effect. In addition, clarifying the temporal dynamics of the RS of an SSVEP response can have important practical consequences, allowing optimization of the paradigms used to capture this response. For instance, if RS is completed within a few hundreds of milliseconds, shorter trials could be used to measure this phenomenon.

Previous studies with low level visual stimuli have shown only a relatively slow RS effect on the SSVEP response. Heinrich and Bach (2001) showed an initial increase in SSVEP amplitude during the first 6 s of a checkerboard reversal stimulation, followed by an exponential decrease for about 10 s and a constant (linear) decline until the end of the 60 s trial. Peachey et al. (1994) presented vertical sinusoidal gratings that reversed contrast (70%) in a square-wave fashion for 20 s (preceded by a 10 s baseline of either a uniform adapting field or an adapting grating). With very low spatial frequencies, SSVEP amplitude remained stable throughout the trial, but higher spatial frequencies initially increased from 6 to 12 s, and then substantially linearly decreased to levels that were about 50% of the amplitude reached earlier in the trial. However,

these latter studies used simple visual stimuli only. Moreover, they considered the absolute amplitude of the SSVEP over time, without comparing the amplitude between repeated and non-repeated stimulus sequences, and so could not disentangle the effects of specific stimulus repetition from general habituation responses. A recent study reported a decrease of the 12 Hz SSVEP response over low-level visual areas for repeated compared to novel complex stimuli (Martens and Gruber, 2012); however, the SSVEP response was only obtained with a single 3000 ms trial, i.e., a trial containing only 36 stimulus presentations. Hence, this study, or other studies to the best of our knowledge, did not address the question of the temporal dynamics of the RS effect for visual shapes presented at a fast periodic rate.

Here, to address the issue of the temporal dynamics of RS to periodic visual stimulation, we presented a periodic train of different faces at the optimal frequency rate for face discrimination (i.e., 5.88 Hz; Alonso-Prieto et al., 2013), for 15 s, in order to reach a large 5.88 Hz (1 F) periodic visual response. Then, from the 16th second of stimulation onward, the exact same face identity was repeated for 35 s. The expected reduction of the response at the frequency of stimulation was compared to a 35-second sequence in which different faces were presented at each stimulation cycle throughout the entire stimulation sequence.

2. Materials and methods

2.1. Participants

Fifteen healthy adult participants (age 20 to 42, 5 males) with normal or corrected vision participated in the study for payment. All participants were right-handed with the range of Edinburgh handedness inventory (Oldfield, 1971) score of 41–50. All participants demonstrated unimpaired face recognition performance (all scores were above 41/54) in the Benton facial recognition test (Benton et al., 1983). They were all Caucasians, as the face stimuli used in the study, except two participants who reported living in Belgium for at least 10 years prior to the experiment. Written informed consent was obtained from all participants prior to the experiment.

2.2. Stimuli

The stimuli consisted of ninety full-front color pictures of Caucasian faces (45 male) selected from a set of the face photographs (Laguesse et al., 2012). The faces were not familiar to the participants.

2.3. Procedure

After the completion of laterality and face recognition tests, the participants were seated in a light- and sound-attenuated room at a distance of 100 cm from the computer monitor. Stimuli were displayed using a custom-made application (SinStim) running on Matlab (The Mathworks), on a light gray background. Each stimulation sequence consisted in an initial 15 s baseline sequence of where different identities were presented, followed by a 35 s sequence of either the same or different identities (i.e., 2 conditions). The frequency of the stimulation was 5.88 Hz (1 F), chosen based on previous observations that this frequency rate provides the largest difference between sequences of different and repeated faces (Alonso-Prieto et al., 2013). The stimulation function was sinusoidal, so that each pixel reached the full luminance value of the face stimulus after half a cycle ((1000/5.88)/2). Since the refresh rate of the CRT monitor was 100 Hz, a full cycle consisted of 17 screen presentations.

In the *same* face condition, the same face, chosen randomly for each participant, was presented repeatedly. During *different* faces sequence, the 45 individual faces of the same sex were used and presented in a new random order in each sequence, from the 16th second until the end of the sequence (50 s in total, Fig. 1). Given that 45 pictures of faces were used and that the number of faces presented was high (i.e.
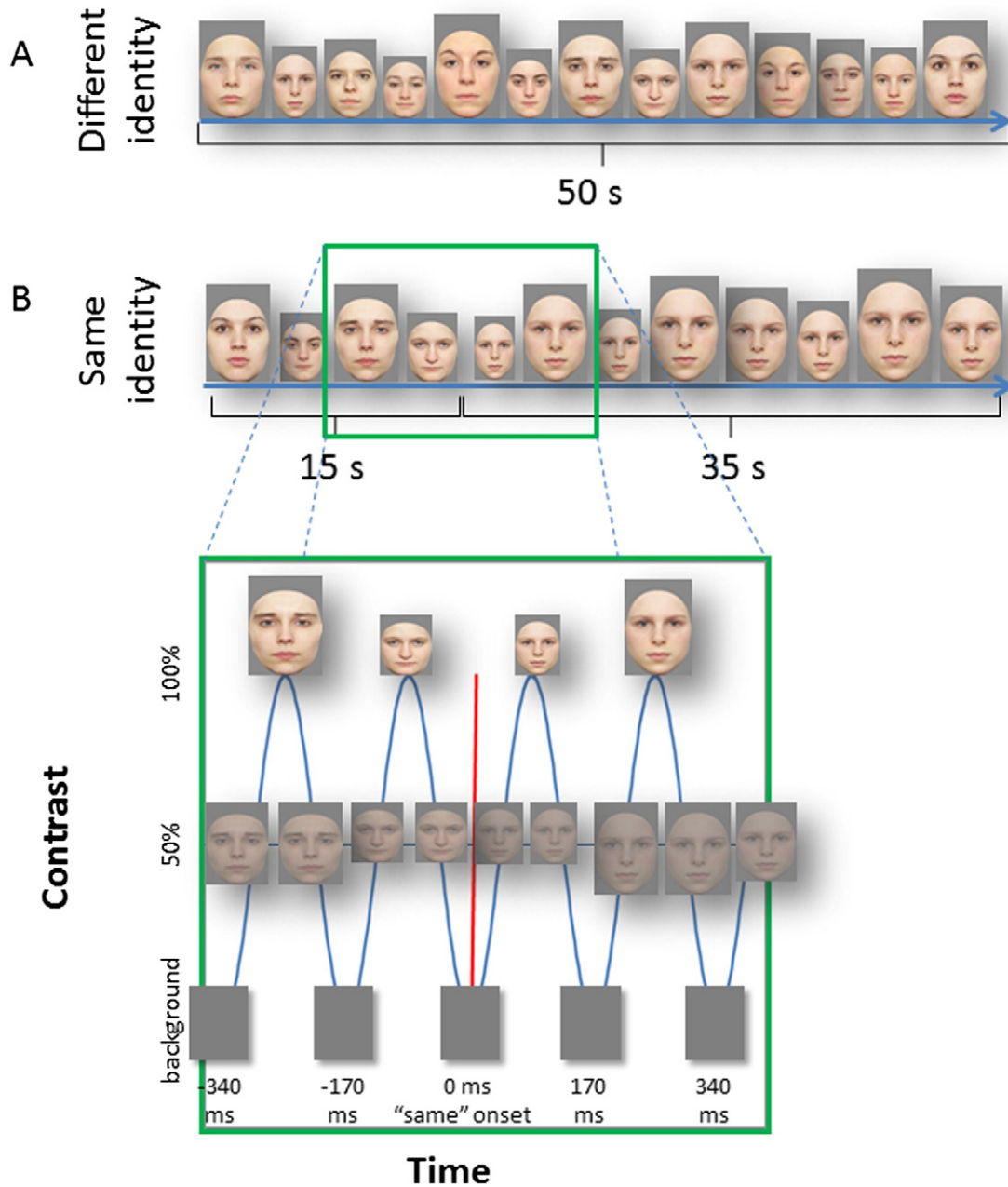
Fig. 1. (A) *Different* condition: different individual faces appear at each stimulation cycle (about 170 ms). (B) *Same* condition: for 15 s, different faces are also presented at each cycle. Then the same face is presented at each cycle until the end of the sequence. The figure illustrates the pattern of stimulation, not the actual number of faces presented in the experiment. The zoom-in shows four cycles around the 15th second, with examples of 0, 50% and 100% contrasts faces. Note that in both conditions face size randomly changed between 88% and 112% between cycles to prevent pixel-based adaptation.

about 200 faces in 35 s), individual faces were repeated during the *different* faces sequence. However, the program controlled that the same face identity did not appear twice in a row. Moreover, a previous study in our laboratory has shown that the amplitude is identical for 10 or 100 different faces used in such sequences, as long as there are no consecutively repeated faces in the sequence (Alonso-Prieto et al., 2013). In addition, to ensure generalization of the RS across low-level changes, the face stimuli changed in size at each presentation cycle (random size between 88% and 112% of base face size, Rossion and Boremanse, 2011). The stimuli subtended 3.44° horizontally and 5.74° vertically at their maximum size (112%). There were thirty 50-s stimulation sequences for each of the two conditions. In 15 sequences female faces were presented and in other fifteen sequences male faces were presented. The order of conditions was random across the participants.

The total duration of the experiment was 75 minutes including a few minutes accumulated in short pauses between each experimental sequence.

To ensure that participants maintained a constant level of attention, an orthogonal task was employed, as in previous studies (e.g., Rossion and Boremanse, 2011). During each sequence, the participants were instructed to fixate on a small black cross located at a typical fixation point for face identification slightly below the bridge of the nose in the center of the face. The fixation cross changed color (to red) briefly (200 ms) five times during each sequence and participants were instructed to detect the color changes by pressing a response key. A response within 1500 ms was considered to be correct. To ensure that subjects were fully concentrated on the sequences, epochs in which performance on the color detection task was lower than 80% correct were
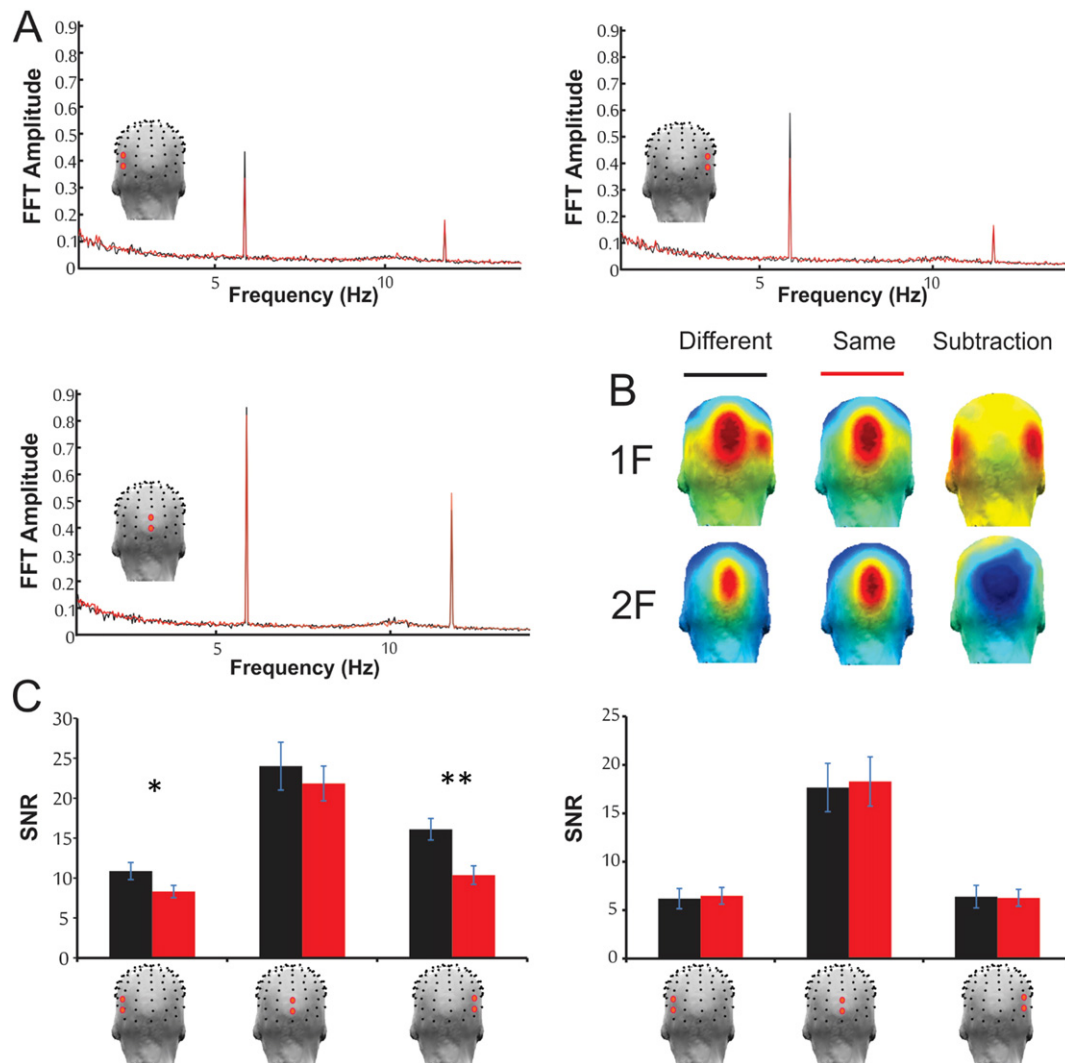
Fig. 2. Grand-averaged results. (A) FFT EEG spectra for three regions of interests: left and right occipito-temporal and medial occipital areas. (B) Topography of the fundamental frequency (1 F, 5.88 Hz) and its second harmonic (2 F = 11.76 Hz) for both conditions and for their subtraction (*different* and *same*). Note the robust frequency-locked response at the 1 F and 2 F, and the larger amplitude for the *different* faces condition at the occipito-temporal sites. (C) Comparison of SNR between these three regions; 1 F (5.88 Hz) is on the left and 2 F (11.76 Hz) is on the right. * $P < 0.05$. ** $P < 0.01$.

removed prior to EEG analysis. The average number of epochs per subject retained in the analyses was 26.3 (88%) and 25.6 (85%) in the *different* and *same* conditions, respectively. There was no difference between *same* and *different* conditions in accuracy ($P > 0.105$). In both conditions, the average response time was 459 ms.

2.4. EEG recording

Continuous electroencephalogram (EEG) was acquired through the ActiveTwo Biosemi electrode system (Biosemi, Amsterdam, Netherlands) from 128 scalp electrodes, digitized at 512 Hz, with the ground formed by the common mode sense active electrode and the driven right leg passive electrode (for more detailed information: http://www.biosemi.com/faq/cms&drl.htm). Eye movements were monitored using four external electrodes placed at the outer canthi of the eyes and above and below the right eye.

2.5. EEG pre-processing

Off-line analysis was performed using the Letswave 5 toolbox (http://nocions.webnode.com) and custom functions in Matlab R2009b (The Mathworks). Individual EEG data recording was first

band-pass filtered between 0.1 and 36 Hz (Butterworth filter with a slope of 24 dB/oct). Next, continuous EEG was segmented into epochs, including 2 s of EEG data before stimulus presentation. Channels with artifacts exceeding 200 μV were interpolated. No more than 6% of the channels per condition were interpolated per participant. Then all channels were re-referenced to a common average, excluding ocular electrodes. Finally the epochs were separated according to the different experimental conditions.

2.6. Frequency-domain analysis

A frequency domain analysis was performed to quantify the magnitude of the repetition suppression effect. The first 19 s of recording in each epoch were discarded. This excluded period consisted of the 2 s pre-stimulation period, the 15 s of the initial adaptation stage (*different* faces period) and, for frequency-domain analysis only, the first 2 s of the test stage. The first 2 s of the test stage were removed in order to exclude transient ERP effects, in line with previous studies (e.g., Rossion and Boremanse, 2011; Alonso-Prieto et al., 2013). Each epoch was then cropped to contain exactly 147 cycles of 1 F (about 25 s), which results in a conveniently high frequency resolution of 0.04 Hz. Then epochs were averaged for each participant and condition. A fast Fourier
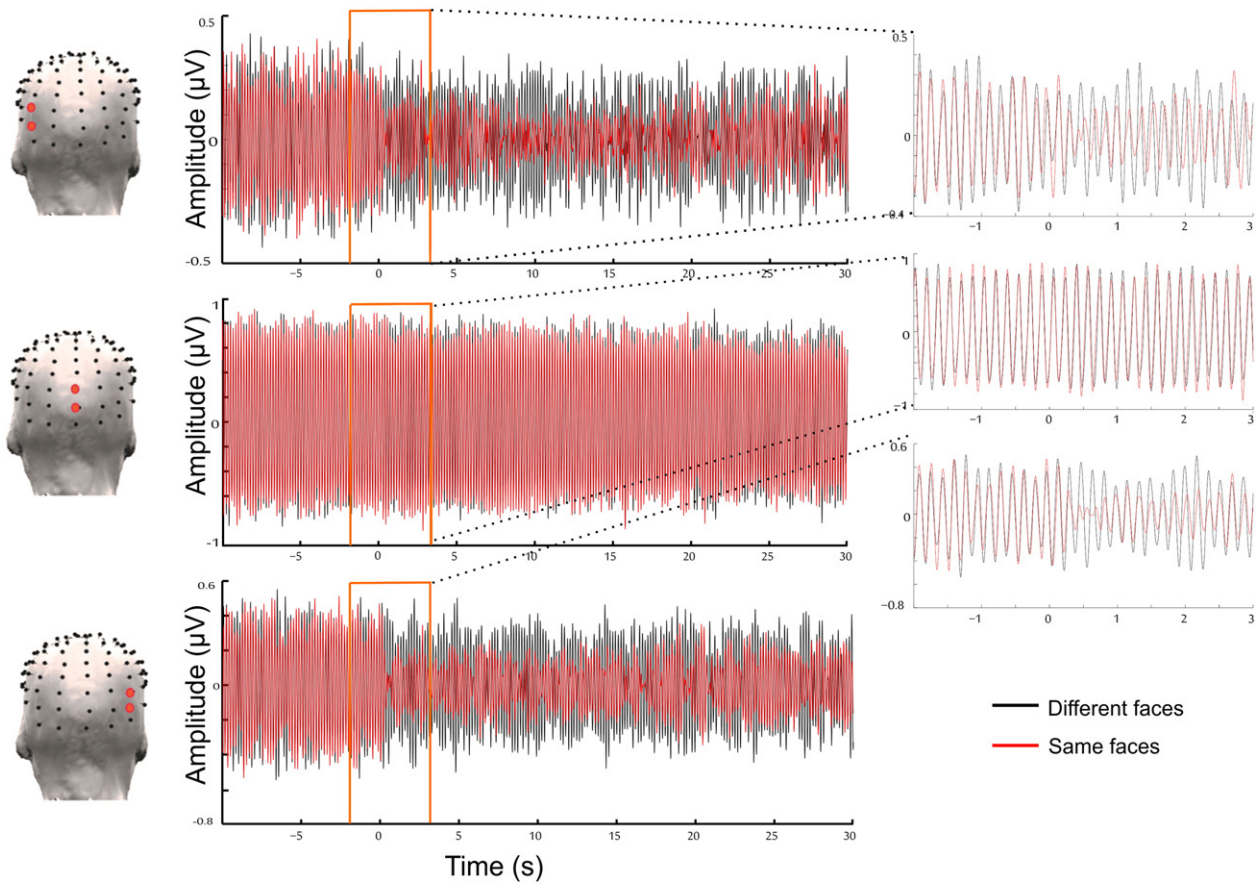
Fig. 3. Illustration of the repetition suppression effect at stimulation frequency over the three ROIs. EEG data was band pass filtered between 4.88 Hz and 6.88 Hz (Butterworth filter with a slope of 24 dB/octave). The decrease of EEG power occurs almost immediately following the beginning of the *same* face stimulation and is much more pronounced at the right than at the left occipito-temporal electrodes.

transform (FFT) was applied to the cropped signals. Signal-to-noise ratio (SNR) was computed at each channel for all available frequencies as the running ratio of the amplitude of a given frequency to the average of the 20 neighboring bins, skipping two neighboring bins at each side and the bins with maximum and minimum amplitude (Rossion et al., 2012). Based on the scalp topography obtained in the present study and our previous studies (e.g., Rossion and Boremanse, 2011), three regions of interest (ROI) were defined to extract and compare amplitude and SNR values: medial occipital (electrodes POOz and Oz), left occipito-temporal (PO7 and PO9) and right occipito-temporal (PO8 and PO10). A two-way repeated measures ANOVA with condition (2: *same and different*) X region (2: *medial*, *left* or *right*) as factors was used. Post hoc tests were Bonferroni-corrected for multiple comparisons. *P*-values below 0.05 were considered significant, and corrected using the Greenhouse–Geisser method where it was appropriate.

2.7. Time-frequency analysis

We first illustrate in Fig. 4 the frequency specificity of the repetition suppression effect by computing a time-frequency representation of the EEG signal during periodic stimulation. To achieve this we used a Morlet wavelet transform with parameters allowing for a high frequency resolution (i.e. 20 Hz central frequency mother wavelet; Full width at half maximum (FWHM) in the frequency-domain = 2.5 Hz at 20 Hz and 0.73 Hz at 5.88 Hz; FWHM in the time-domain = 0.350 s at 20 Hz and 1.2 s at 5.88 Hz). This computation was applied on pre-processed EEG epochs that were averaged across trials for each subject and condition.

Next, we used a Morlet wavelet approach to quantify the temporal dynamics of the repetition suppression effect by computing the amplitude envelope of the EEG signal across time exactly at the stimulation

frequency (5.88 Hz). Specifically, in each subject, we first averaged individual EEG epochs by condition, and the amplitude of the 5.88 Hz response was computed (using a 7 Hz central frequency wavelet, see below for FWHM) at each time bin from -16 s to 35 s relative to the onset of the change in the stimulation sequence. The resulting amplitude envelopes were cropped to [-13 s to 32 s] to remove edge effects from the time-frequency analysis and baseline corrected by subtracting the mean amplitude in a [-10 s to -1 s] time-window. To quantify the onset latency of the RS effect, a *Z*-score was computed for each time bin of the amplitude envelope [-10 s to 30 s] in the *same* condition against the amplitude envelope in a 10 s-long moving window of the *different* condition centered on the current time bin. The earliest latency at which *Z*-scores significantly deviated from zero was assessed using a percentile bootstrap test (sampling subjects with replacement) with 5000 resampling performed at every time bin. To take into account the problem of multiple comparisons and the non-independence of consecutive time bins, we used a conservative significance level of 0.01 (two-tailed) and only considered significant responses that lasted for at least 0.1 s. In this analysis, the estimation of the onset latency of the RS effect depends on the temporal spread of the mother wavelet used for the time-frequency analysis. To evaluate how the wavelet temporal spread (defined by the time-domain standard deviation of the Gaussian in the wavelet function) affected the estimate of the RS onset latency (at the stimulation frequency of 5.88 Hz), we measured this onset latency using multiple wavelet temporal spreads (i.e. standard deviation of the Gaussian: 0.064 s to 0.214 s at the central frequency of 7 Hz, i.e. temporal resolution of 90 to 300 ms respectively, which corresponds to half of the FWHM of the wavelet at 5.88 Hz).

Last, to further characterize the temporal dynamics of the RS effect, we evaluated its overall trend over time from its onset to the offset of
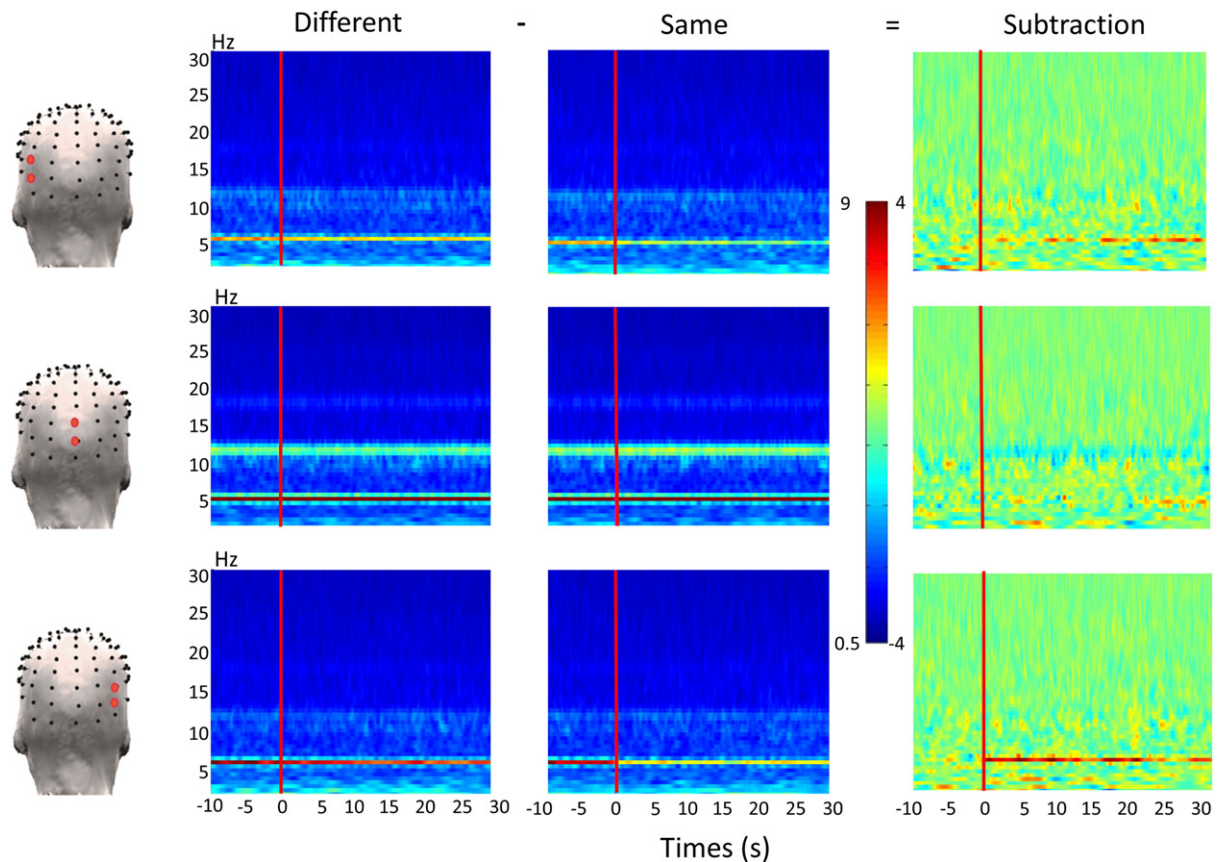
Fig. 4. Time-frequency decomposition based on the Morlet wavelet transform averaged across all participants. The response is centered on the frequency of stimulation (1 F, 5.88 Hz) and its second harmonic (2 F, 11.76 Hz). The 1 F response is particularly large over occipital medial sites, but it does not show adaptation in this condition, remaining stable in amplitude until the end of the sequence. The RS effect with face repetition is visible over the lateral ROIs and it is much more prominent on the right side.

the sequence. To do this we computed the slope of the RS effect by fitting a line to the *Z*-scored data representing the deviation of the *same* condition relative to the *different* condition (see above). This was done for each subject and a one-sample t-test was used to determine whether the slope was significantly different from zero. For this we used a 7 Hz central frequency wavelet with temporal spread of 0.15 s at central frequency (i.e. spread of 0.179 s at 5.88 Hz; FWHM/2 = 0.21 s). Furthermore, to disentangle amplitude trends arising from adaptation to facial identity from trends related to a non-specific amplitude variation of the periodic response, we computed the same trend analyses as for the RS effect but directly on the 5.88 Hz amplitude envelopes for the *same* and *different* conditions.

3. Results

3.1. Periodic EEG response in the frequency domain and time-frequency display

The periodic EEG response was visible at narrow frequency bands of 0.04 Hz at the exact 5.88 Hz stimulation frequency (1 F) and up to the seventh harmonic of this frequency (i.e., 5.88 Hz x 7 = 41.2 Hz) (Fig. 2). Time-frequency analysis shows that the effect is confined to the narrow frequency band of stimulation (Fig. 3). Across all channels the response at the fundamental frequency and its first three harmonics was at least two standard deviations higher than the responses at the 20 surrounding frequency bins (noise). For these harmonics, in both conditions the largest amplitude was observed at the medial occipital sites, with the largest responses observed at electrodes POOz and Oz (Fig. 2). At 1 F only, a significant and spatially separated locus of activation was also observed at occipito-temporal sites, most prominently on the right hemisphere (channels PO8 and PO10). In line with previous

observations, at 6 Hz of stimulation frequency, there was no evidence of a repetition suppression effect at the second harmonic (12 Hz) and subsequent harmonics (e.g., 3f = 18 Hz, etc.) (Alonso-Prieto et al., 2013), which were not analyzed further.

A two-way repeated measures ANOVA yielded a main effect of condition ($F(1,14) = 19.35$, $P = 0.001$) and a significant interaction between region (*medial, left* or *right*) and condition (*same* or *different*) ($F(2,28) = 3.91$, $P = 0.032$). Importantly, a highly significant RS effect was found: post-hoc comparisons showed that *different* stimulation led to a larger amplitude than the identical faces at the occipito-temporal ROIs on the left ($P < 0.009$) and on the right ($p < 0.001$), whereas no difference was found at the medial ROI ($p = 0.49$), replicating previously reported RS effects (Rossion and Boremanse, 2011; Rossion et al., 2012; Alonso-Prieto et al., 2013).

For consistency with previous studies (e.g., Rossion et al., 2012), we performed a similar analysis with SNR values (Fig. 2C). A two-way repeated measure ANOVA yielded main effects of *region* ($F(2,28) = 14.92$, $P < 0.001$) and *condition* ($F(1,14) = 24.21$, $P < 0.001$) and a significant interaction between the two factors ($F(2,28) = 3.65$, $P = 0.039$). The subsequent analysis that excluded the medial occipital region yielded an effect of *region* ($F(1,14) = 7.52$, $P = 0.016$), with the right hemisphere yielding higher SNR values than the left, and an effect of *condition* (*different > same*, $F(1,14) = 31.46$, $P < 0.001$), and a significant interaction between the two factors ($F(1,14) = 7.57$, $P < 0.016$), indicating a larger RS effect in the right than the left hemisphere.

3.2. Time-domain analysis

Fig. 3 illustrates the modulation across time of the response at the stimulation frequency. Introducing the *same* face presentation after 15 s of showing different faces produced a significant and abrupt

decrease in the amplitude of the response at stimulation frequency (i.e. the RS effect), with no further decrease until the end of the sequence: the zoom-in around the time of change suggests that the decrease in response amplitude occurs within 1 s following the beginning of the *same* faces stimulation (Fig. 3).

In order to quantitatively assess the temporal characteristics of the RS effect, the signal amplitude envelope at stimulation frequency (1 F) was computed using a wavelet approach and then transformed into *Z*-scores as detailed in Sec. 2. At the right occipito-temporal ROI, following the introduction of *same* faces, the earliest significant RS effect ($P < 0.01$, two-tailed) varied from 747 ms (wavelet with temporal resolution -FWHM/2 - of 90 ms) to 211 ms (wavelet with temporal resolution -FWHM/2 - of 300 ms) at the right occipito-temporal ROI and lasted for 730 to 1280 consecutive ms (for the highest and lowest temporal resolution wavelet respectively)(Fig. 5). This confirms that the RS effect starts well within 1 s of the introduction of the *same* face stimulation. At the left occipito-temporal ROI the RS effect started at 3100 ms to 3060 ms and lasted for 100 to 400 consecutive ms for the highest and lowest temporal resolution wavelet respectively. There was no significant RS effect at the medial occipital ROI.

In addition, while the onset of the RS effect was rapid and abrupt, especially in the right hemisphere, its magnitude tended to decrease over time until the end of the sequence in that hemisphere (Fig. 5). This was evidenced by the finding that the slope of the line fitted to the *Z*-scored data (from 0.42 s to 32 s relative to the onset of the change in the sequence) was significantly positive for the right hemisphere (slope: 0.023 ± 0.027, t(14) = 3.4, $P < 0.005$, Fig. 5). For the left hemisphere, the slope (line fitted from 2.97 s to 32 s) was not significantly

different from zero (slope: -0.005 ± 0.03, t(14) = -0.57, $P = 0.6$). Considering separately the amplitude trend across time in the right hemisphere for the *same* and *different* conditions revealed a significant amplitude decrease in the *different* condition (slope: -0.48 ± 0.59, t(14) = 3.16, $P < 0.01$), while in the *same* condition, reflecting the RS effect, the amplitude remained stable from the onset of the adaptation until the end of the sequence (slope: 0.13 ± 0.72, t(14) = 0.7, $P = 0.5$). This indicates that the overall reduction of the RS effect over time observed in the right hemisphere is due to a non-specific (i.e. not related to face identity adaptation) amplitude reduction taking place in the *different* condition. In the left hemisphere, the overall amplitude tended to be stable for both *same* (slope: -0.29 ± 1.1, t(14) = -1, $P = 0.32$) and *different* (slope: -0.06 ± 0.50, t(14 = -0.46, $P = 0.65$) conditions.

4. Discussion

The current study replicates the repetition suppression (RS) effect, i.e., the reduction of the EEG response over the occipito-temporal cortex at the fundamental frequency rate, found when identical face identities are presented (Alonso-Prieto et al., 2013; Rossion and Boremanse, 2011; Rossion et al., 2012). Such an RS effect is observed despite substantial variations of stimulus size at every cycle, indicating that it is not due to a mere repetition of low-level visual information. Here, this identity-specific RS effect was obtained by presenting first a sequence of different face identities and then abruptly introducing the repetition of the same identity. The main observation was that, over the right hemisphere, the decrease of 5.88 Hz response following the introduction of identical faces was abrupt, reaching its lowest level within a
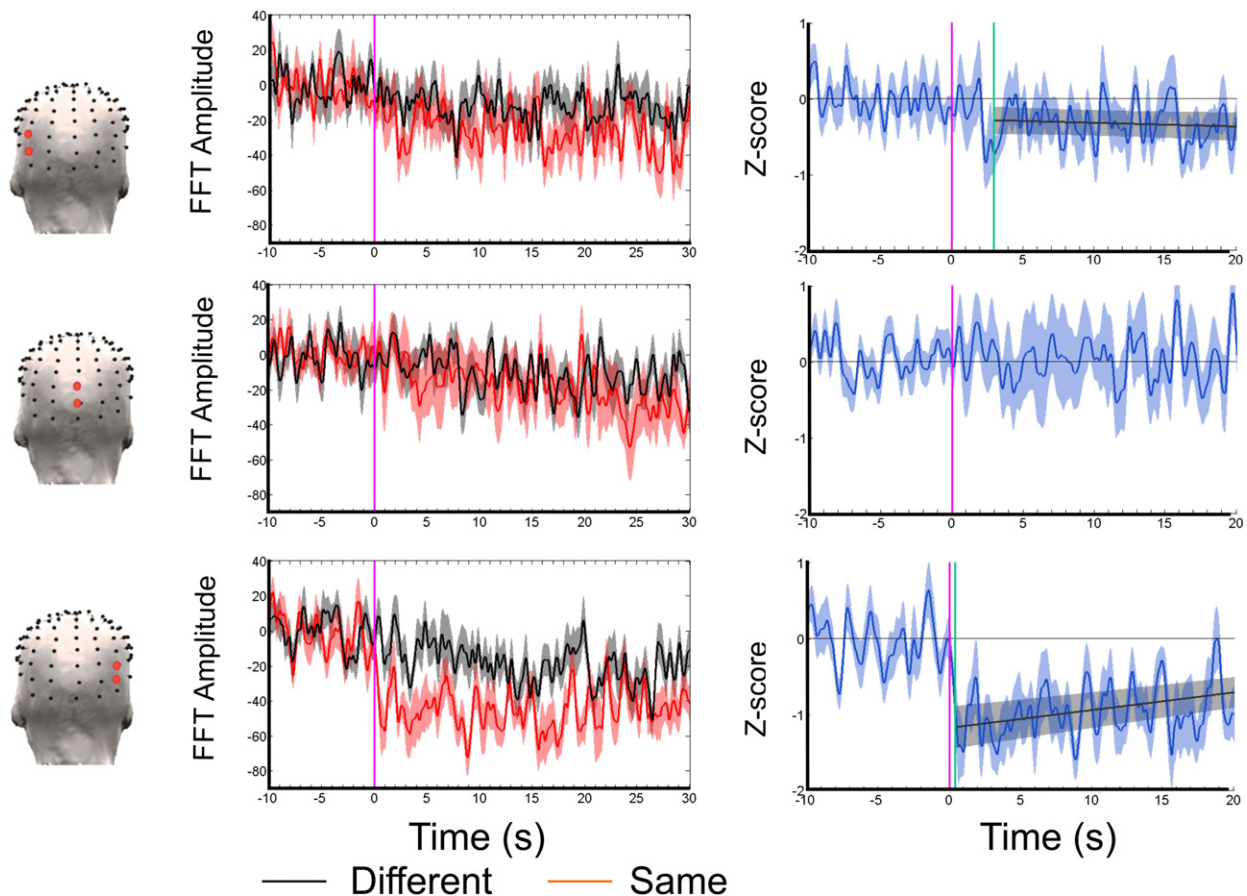

Fig. 5. Left: Grand-averaged amplitude envelopes of the wavelet analysis at the fundamental frequency (1 F, 5.88 Hz) for both conditions at each ROI. On the right are the corresponding grand-averaged *Z*-scored amplitudes, calculated for each time point in the *same* face condition against a 10-s long moving window in the *different* faces condition. The shaded area represents the standard error of the mean. The first significant difference appears at 211 ms after *same*-identity stimulation in the right hemisphere (for the wavelet with the highest frequency resolution). The lines fitted to the *Z*-scored amplitudes in each subjects to estimate the overall trend of the adaptation effect are showed for the left and right hemisphere ROIs (where the adaptation effect was significant) using the parameters averaged across subjects.

few hundreds of milliseconds and remaining at a stable low level until the end of the sequence.

Assuming that adaptation reflects the discrimination ability of the neuronal population encoding facial identity, a rapid RS effect is consistent with the fast nature of individual face discrimination (i.e., within the first two saccades, Peterson and Eckstein, 2012; Hsiao and Cottrell, 2008). It is also consistent with the latency of the effects obtained in transient ERP studies (e.g., Caharel et al., 2009a; Heisz et al., 2006; Itier and Taylor, 2002; Jacques et al., 2007; Jemel et al., 2003), which can be observed only in the right hemisphere in some studies (Caharel et al., 2009b; Jacques et al., 2007). That is, a single repetition of face following a brief time interval is sufficient to elicit a difference from the response elicited by a non-repeated face at around 170 ms after repeated stimulus presentation ("N170" component, see Rossion and Jacques, 2011). Although with the transient ERP approach utilized in these latter studies the effects of stimulus repetition cannot be unambiguously characterized as reflecting RS, the correspondence between the effects obtained during transient and fast periodic visual stimulation is further supported by the similarity of their scalp topographies. That is, the RS effect, i.e. subtraction of *different* and *same* conditions, in both approaches, tends to be localized over the occipito-temporal cortex, with a right hemispheric dominance (e.g., compare the effects observed in Jacques et al., 2007 with the present study). Thus, while the neural sources of the transient ERP components and rapid periodic visual responses to faces could be different, these effects may be driven by the same face identity-coding populations.

The neurocomputational mechanism of the RS is not yet clear. A number of models have been put forward to account for this phenomenon (Grill-Spector et al., 2006), among them models based on predictive coding or perceptual inference (Lieder et al., 2013; Summerfield et al., 2008). While the current study was not designed to differentiate between these models, the fast nature of the RS effect, at least in the right hemisphere, and the fact that it is limited to the periodic frequency of stimulation and to the occipito-temporal cortex favor a bottom-up interpretation, in which signal change is driven by the stimulus rather than by top-down expectations. However, in the left hemisphere the RS effect was not only lower, as in previous studies (e.g., Rossion et al., 2012; Alonso-Prieto et al., 2013) but also emerged significantly after several seconds only, suggesting that it might be driven by top-down expectations or by inputs from the right hemisphere. Moreover, although it is well established that spatial and selective attention modulate the SSVEP (e.g. Morgan et al., 1996; Müller et al., 2006; Andersen et al., 2008), the current results are unlikely to be due to attentional modulations, for the following reasons. First, the task required was orthogonal, i.e., no explicit face processing was required and no significant difference between the conditions was found either in accuracy or latency of the behavioral responses. Second, the drop of attention would have to occur immediately following the introduction of identical faces. Although effects of attention can emerge in the SSVEP response after a few hundreds of milliseconds (Müller et al., 1998; Belmonte, 1998), such effects are linked to radical switches of attention elicited by behavioral target discrimination tasks at newly cued locations. Again, here the participants simply had to maintain attention on a fixation cross centered on the face stimulus throughout the entire stimulation. Moreover, whereas SSVEP attentional effects have been reported over medial occipital sites for centrally presented stimuli (Andersen et al., 2008; Andersen and Müller, 2010; Müller et al., 2006), the effects observed here are lateralized over occipito-lateral sites, even though the absolute SSVEP response was largest at medial occipital sites (Fig. 2).

The results also show a long-term adaptation for periodic response in *different* condition, which may lead to a partial attenuation of the identity-specific adaptation effect, when *same* condition is directly compared to *different* condition. Similar slow adaptation process has been previously reported for low level stimuli (Heinrich and Bach, 2001; Peachey et al., 1994). Alternatively, this modest adaptation effect may stem from face-specific changes due to cumulative effects of face presentation, including a small number of non-sequential repetitions of the individual faces. Although the nature of this long-term identity non-specific adaptation cannot be determined in this study, this effect underscores the importance of keeping adaption trials within FPVS paradigm relatively short in order to avoid attenuation of the effects. Importantly, the analysis of power changes following the onset of the same-identity stimulation indicates that there is no additional, long term adaptation of the response, emphasizing the fast and complete nature of the identity-specific RS.

5. Conclusions

The present study showed a rapid, complete and frequency-specific repetition suppression effect for the SSVEP elicited by face identity over the right hemisphere, with a reduced and slower effect in the left hemisphere. While the neuronal mechanisms of this effect require further clarification, the results of the current study show the high capacity of the human visual system for fast discrimination between different face identities and generalization of the same identity over a range of different sizes of the same face. Importantly, the SSVEP discrimination response is obtained here at an objective narrow frequency band, with a high SNR, and while the participants perform an orthogonal task. The present results also have important methodological implications, showing that the fast periodic visual stimulation paradigm can be used with short stimulation durations to capture robust face identity adaptation effects.

References

Adrian, E.D., Matthews, B.H.C., 1934. The Berger rhythm: potential changes from the occipital lobes in man. Brain 4 (57), 355–385.

Alonso-Prieto, E., Van Belle, G., Liu-Shuang, J., Norcia, A.M., Rossion, B., 2013. The 6 Hz fundamental stimulation frequency rate for individual face discrimination in the right occipito-temporal cortex. Neuropsychologia 51 (13), 2863–2875.

Andersen, S.K., Müller, M.M., 2010. Behavioral performance follows the time course of neural facilitation and suppression during cued shifts of feature-selective attention. Proc. Natl. Acad. Sci. U. S. A. 107 (31), 13878–13882. http://dx.doi.org/10.1073/pnas.1002436107.

Andersen, S.K., Hillyard, S.A., Müller, M.M., 2008. Attention facilitates multiple stimulus features in parallel in human visual cortex. Curr. Biol. 18 (13), 1006–1009. http://dx.doi.org/10.1016/j.cub.2008.06.030.

Andrews, T.J., Ewbank, M.P., 2004. Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. Neuroimage 23, 905–913.

Baylis, G.C., Rolls, E.T., 1987. Responses of neurons in the inferior temporal cortex in short term and serial recognition memory tasks. Exp. Brain Res. 65 (3), 614–622.

Belmonte, M., 1998. Shifts of visual spatial attention modulate a steady-state visual evoked potential. Cogn. Brain Res. 6, 295–307.

Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. J. Cogn. Neurosci. 8 (6), 551–565.

Benton, A.L., Sivan, A.B., Hamsher, K.D., Varney, N.R., Spreen, O., 1983. Visual Form Discrimination. In Contributions to Neuropsychological Assessment. Oxford University Press, New York, USA.

Caharel, S., D'Arripe, O., Ramon, M., Jacques, C., Rossion, B., 2009a. Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: evidence from the N170 ERP component. Neuropsychologia 47 (3), 639–643.

Caharel, S., Jiang, F., Blanz, V., Rossion, B., 2009b. The human brain recognizes individual faces faster from shape than surface reflectance diagnostic information. J. Vis. 9 (8), 548.

Eimer, M., Gosling, A., Nicholas, S., Kiss, M., 2011. The N170 component and its links to configural face processing: a rapid neural adaptation study. Brain Res. 1376, 76–87.

Ewbank, M.P., Henson, R.N., Rowe, J.B., Stoyanova, R.S., Calder, A.J., 2013. Different neural mechanisms within occipitotemporal cortex underlie repetition suppression across same and different-size faces. Cereb. Cortex 23, 1073–1084.

Fahy, F.L., Riches, I.P., Brown, M.W., 1993. Neuronal activity related to visual recognition memory: long-term memory and the encoding of recency and familiarity

information in the primate anterior and medial inferior temporal and rhinal cortex. Exp. Brain Res. 96 (3), 457–472.

Gerlicher, A.M.V., van Loon, A.M., Scholte, H.S., Lamme, V.A.F., van der Leij, A.R., 2013. Emotional facial expressions reduce neural adaptation to face identity. Soc. Cogn. Affect. Neurosci. 9 (5), 610–614.

Gilaie-Dotan, S., Nir, Y., Malach, R., 2008. Regionally-specific adaptation dynamics in human object areas. NeuroImage 39 (4), 1926–1937.

Grill-Spector, K., Malach, R., 2001. FMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol. 107 (1-3), 293–321.

Grill-Spector, K., Henson, R.N., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn. Sci. 10 (1), 14–23.

Gruber, T., Malinowski, P., Müller, M.M., 2004. Modulation of oscillatory brain activity and evoked potentials in a repetition priming task in the human EEG. Eur. J. Neurosci. 19 (4), 1073–1082.

Heinrich, S.P., Bach, M., 2001. Adaptation dynamics in pattern-reversal visual evoked potentials. Documenta ophthalmologica. Adv. Ophthalmol. 102 (2), 141–156.

Heisz, J.J., Watter, S., Shedden, J.M., 2006. Progressive N170 habituation to unattended repeated faces. Vis. Res. 46 (1-2), 47–56.

Henson, R.N., Shallice, T., Gorno-Tempini, M.L., Dolan, R.J., 2002. Face repetition effects in implicit and explicit memory tests as measured by fMRI. Cereb. Cortex 12 (2), 178–186.

Hsiao, J.H., Cottrell, G., 2008. Two fixations suffice in face recognition. Psychol. Sci. 19, 998–1006.

Itier, R.J., Taylor, M.J., 2002. Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. Neuroimage 15, 353–372.

Jacques, C., D'Arripe, O., Rossion, B., 2007. The time course of the inversion effect during individual face discrimination. J. Vis. 7, 1–9.

Jemel, B., Schuller, A.-M., Cheref-Khan, Y., Goffaux, V., Crommelinck, M., Bruyer, R., 2003. Stepwise emergence of the face-sensitive N170 event-related potential component. Neuroreport 14, 2035–2039.

Jonas, J., Rossion, B., Krieg, J., Koessler, L., Colnat-Coulbois, S., Vespignani, H., Jacques, C., Vignal, J.P., Brissart, H., Maillard, L., 2014. Intracerebral electrical stimulation of a face-selective area in the right inferior occipital cortex impairs individual face discrimination. NeuroImage 99, 487–497. http://dx.doi.org/10.1016/j.neuroimage.2014.06.017.

Kovács, G., Zimmer, M., Bankó, E., Harza, I., Antal, A., Vidnyánszky, Z., 2006. Electrophysiological correlates of visual adaptation to faces and body parts in humans. Cereb. Cortex 16 (5), 742–753.

Laguesse, R., Dormal, G., Biervoye, A., Kuefner, D., Rossion, B., 2012. Extensive visual training in adulthood significantly reduces the face inversion effect. J. Vis. 12 (10), 1–13.

Li, L., Miller, E.K., Desimone, R., 1993. The representation of stimulus familiarity in anterior inferior temporal cortex. J. Neurophysiol. 69 (6), 1918–1929.

Lieder, F., Daunizeau, J., Garrido, M.I., Friston, K.J., Stephan, K.E., 2013. Modelling trial-by-trial changes in the mismatch negativity. PLoS Comput. Biol. 9 e1002911.

Martens, U., Gruber, T., 2012. Sharpening and formation: two distinct neuronal mechanisms of repetition priming. Eur. J. Neurosci. 36 (7), 2989–2995.

Merzagora, A.R., Coffey, T.J., Sperling, M.R., Sharan, A., Litt, B., Baltuch, G., Jacobs, J., 2014. Repeated stimuli elicit diminished high-gamma electrocorticographic responses. NeuroImage 85 (2), 844–852.

Miller, E.K., Gochin, P.M., Gross, C.G., 1991. Habituation-like decrease in the responses of neurons in inferior temporal cortex of the macaque. Vis. Neurosci. 7 (4), 357–362.

Morgan, S.T., Hansen, J.C., Hillyard, S.A., 1996. Selective attention to stimulus location modulates the steady-state visual evoked potential. Proc. Natl. Acad. Sci. U. S. A. 93 (10), 4770–4774.

Müller, M.M., Teder-Sälejärvi, W., Hillyard, S.A., 1998. The time course of cortical facilitation during cued shifts of spatial attention. Nat. Neurosci. 1 (7), 631–634.

Müller, M.M., Andersen, S., Trujillo, N.J., Valdés-Sosa, P., Malinowski, P., Hillyard, S.A., 2006. Feature-selective attention enhances color signals in early visual areas of the human brain. Proc. Natl. Acad. Sci. U. S. A. 103 (38), 14250–14254. http://dx.doi.org/10.1073/pnas.0606668103.

Norcia, A.M., Appelbaum, G., Ales, J., Cottereau, B., Rossion, B., 2015. The steady state visual evoked potential in vision research: a review. J. Vis. 15 (4). http://dx.doi.org/10.1167/15.6.4.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9 (1), 97–113.

Peachey, N.S., Demarco, P.J., Ubilluz, R., Yee, W., 1994. Short-term changes in the response characteristics of the human visual evoked potential. Vis. Res. 34 (21), 2823–2831.

Peterson, M.F., Eckstein, M.P., 2012. Looking just below the eyes is optimal across face recognition tasks. Proc. Natl. Acad. Sci. U. S. A. 109, E3314–E3323.

Regan, D., 1966. Some characteristics of average steady-state and transient responses evoked by modulated light. Electroencephalogr. Clin. Neurophysiol. 20 (3), 238–248.

Regan, D., 1989. Human Brain Electrophysiology: Evoked Potentials and Evoked Magnetic Fields in Science and Medicine. Appleton & Lange.

Ringo, J.L., 1996. Stimulus specific adaptation in inferior temporal and medial temporal cortex of the monkey. Behav. Brain Res. 76 (1), 191–197.

Rossion, B., 2014. Understanding individual face discrimination by means of fast periodic visual stimulation. Exp. Brain Res. 232, 1599–1621.

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. J. Vis. 11, 1–21.

Rossion, B., Jacques, C., 2011. The N170: Understanding the Time-Course of Face Perception in the Human Brain. In: Luck, S., Kappenman, E. (Eds.), The Oxford Handbook of ERP Components. Oxford University Press, pp. 115–142.

Rossion, B., Prieto, E.A., Boremanse, A., Kuefner, D., Van Belle, G., 2012. A steady-state visual evoked potential approach to individual face perception: effect of inversion, contrast-reversal and temporal dynamics. Neuroimage 63 (3), 1585–1600.

Summerfield, C., Trittschuh, E.H., Monti, J.M., Mesulam, M.M., Egner, T., 2008. Neural repetition suppression reflects fulfilled perceptual expectations. Nat. Neurosci. 11 (9), 1004–1006.

Vakli, P., Németh, K., Zimmer, M., Kovács, G., 2014. The face evoked steady-state visual potentials are sensitive to the orientation, viewpoint, expression and configuration of the stimuli. Int. J. Psychophysiol. 94, 336–350.

Walther, C., Schweinberger, S.R., Kovács, G., 2013. Adaptor identity modulates adaptation effects in familiar face identification and their neural correlates. PLoS One 8 (8), e70525.