Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials

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Understanding how the human brain discriminates complex visual patterns, such as individual faces, is an important issue in Vision Science. Here we tested sensitivity to individual faces using steady-state visual-evoked potentials (SSVEPs). Twelve participants were presented with 90-s sequences of faces appearing at a constant rate (3.5 faces/s) while high-density electroencephalogram (EEG) was recorded. Fast Fourier Transform (FFT) of EEG showed a large response at the fundamental stimulation frequency (3.5 Hz) over posterior electrode sites. This response was much larger when the face identity changed at that rate (different faces) than when an identical face was repeated. The reduction of signal in the identical face condition was not due to low-level feature adaptation, since it was observed despite changes of stimulus size, and was localized specifically over the right lateral occipital cortex. Moreover, the difference between conditions disappeared when faces were inverted. This first observation of habituation of the SSVEP to repeated face identity in the human brain provides further evidence for face individualization in the right occipito-temporal cortex by means of a simple, fast, and high signal-to-noise approach. Most importantly, it offers a promising tool to study the sensitivity to visual features of individual faces and objects in the human brain.

Introduction

Face recognition requires segmentation of the person's face from the background of the visual scene and the extraction of a visual representation that is sufficiently detailed to allow discrimination of this face from other faces. Faces form a highly visually homogenous category (Galton, 1883), all sharing the same basic shape and surface reflectance (color, texture) properties, at least within the same "race" of faces. Hence, individualization of faces is a particularly difficult task for the human brain. Nevertheless, humans' performance at individualizing faces is surprisingly good (Bahrick, Bahrick, & Wittlinger, 1975; Bruce & Young, 1998; Sergent, 1989). Understanding how the human brain individualizes faces is therefore an important challenge for cognitive neuroscience.

Studies in experimental psychology and psychophysics have aimed at pinpointing *what,* exactly, are the cues that are diagnostic for face individualization, that is the variations in terms of shape and surface reflectance of facial features (eyes, nose, …) and the variations in terms of relative distances between these features (e.g., Gosselin &

Schyns, 2001; Haig, 1984, 1985; O'Toole, Vetter, & Blanz, 1999). These studies have also aimed to understand *how* individual faces are distinguished (holistically/configurally vs. analytically, e.g., Maurer, Le Grand, & Mondloch, 2002; Sergent, 1984; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987).

At the neural level, it is known that face-selective cells in the monkey infero-temporal (IT) cortex discharge at different rates to the presentation of distinct individual faces (Leopold, Bondar, & Giese, 2006; Rolls & Tovee, 1995; Young & Yamane, 1992). In humans, neuroimaging studies have identified several visual areas, from the posterior lateral occipital cortex to the anterior part of the temporal lobe, that respond preferentially or even selectively to faces (Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995; Sergent, Ohta, & MacDonald, 1992; Weiner & Grill-Spector, 2010). These areas, which show a much stronger response in the right than the left hemisphere, are also sensitive to differences between individual faces (e.g., Andrews & Ewbank, 2004; Gauthier et al., 2000; Gilaie-Dotan & Malach, 2007; Grill-Spector & Malach, 2001; Schiltz et al., 2006; Winston, Henson, Fine-Goulden, & Dolan, 2004; Yovel & Kanwisher,

2005). In addition, EEG/MEG studies have shown that the human brain is sensitive to differences between individual faces as early as 160 ms following stimulus onset, within the time window of the occipito-temporal face-sensitive N170/M170 component (e.g., Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Caharel, Jiang, Blanz, & Rossion, 2009; Ewbank, Smith, Hancock, & Andrews, 2008; Heisz, Watter, & Shedden, 2006; Itier & Taylor, 2002; Jacques & Rossion, 2006; Jacques, d'Arripe, & Rossion, 2007; for a review, see Rossion & Jacques, 2011) and also at later latencies (e.g., Paller, Gonsalves, Grabowecky, Bozic, & Yamada, 2000; Schweinberger, Pfutze, & Sommer, 1995; Tanaka, Curran, Porterfield, & Collins, 2006).

To demonstrate sensitivity to individual faces, the majority of the fMRI and EEG/MEG studies cited above have relied on the well-known phenomenon of (visual) neural adaptation, also termed *repetition suppression,* or *habituation,* that is the reduction of neural activity following repetition of the same stimulus (Grill-Spector, Henson, & Martin, 2006; Grill-Spector & Malach, 2001; Henson & Rugg, 2003; Kovács et al., 2006; for earlier studies of stimulus repetition suppression effects in single neurons in monkeys' IT, see Baylis & Rolls, 1987; Brown, Wilson, & Riches, 1987; Li, Miller, & Desimone, 1993; Ringo, 1996). The neural mechanisms of this phenomenon are still unclear (Grill-Spector et al., 2006; Sawamura, Orban, & Vogels, 2006), but it is a useful tool for revealing the sensitivity of the whole system, a population of neurons, a given area, or a specific time window, to a property of a stimulus that is changed vs. kept constant. Concerning sensitivity to individual faces, the rationale is that populations of neurons that are sensitive to differences between individual faces should show a smaller response when the same individual face stimulus is repeated compared to the presentation of different face stimuli. Once the neural substrates of individual face representations have been identified with this method, one can then test which facial cues are particularly diagnostic for face individualization in specific areas and at well-defined time windows, and how individual faces are discriminated and represented in the human brain (e.g., "holistically", Jacques & Rossion, 2009; Rhodes, Michie, Hughes, & Byatt, 2009; Schiltz & Rossion, 2006).

Unfortunately, neuroimaging and scalp electromagnetic recording studies of facial identity adaptation present a number of limitations that are not often mentioned but are well known by researchers relying on these methods. First, neural adaptation effects may be relatively small in magnitude (e.g., about 0.15% percent-signal-change fMRI increase for different faces vs. identical faces in the right fusiform gyrus in Mazard, Schiltz, & Rossion, 2006; Yovel & Kanwisher, 2005; about 1 μV over a 6-μV amplitude for the N170 component in Jacques et al., 2007 and of even lesser magnitude in other studies). Therefore, the acquisition of robust data usually requires a substantial number of participants in a given experiment as well as the collection of data from many trials for each participant, thus resulting in experiments of relatively long duration. Second, neural adaptation effects are quite susceptible to methodological factors such as variations of timing parameters (duration of adapter face(s)), type of stimulation (block stimulation or event-related pairs), and number of individual face repetitions (see Henson & Rugg, 2003; Mazard et al., 2006). In particular, the task performed may have important effects on face identity adaptation effects, in fMRI at least (Grill-Spector et al., 2006; Henson, Shallice, Gorno-Tempini, & Dolan, 2002). Third, ambiguities arise in the quantification of adaptation effects, which is further complicated by the polarity (positive or negative) of the electromagnetic components, and the negative BOLD response in fMRI (i.e., an area may show a larger signal to different faces than identical faces because it is less deactivated for different faces). Finally, assessing face identity adaptation effects requires the resolution of some ambiguities in the definition of individual brain areas of interest in fMRI or time window and components of interests in neuromagnetic measurements.

These issues are important because they could potentially explain discrepancies in the data reported in different studies (e.g., the presence or absence of effects of face identity repetition on N170, see Rossion & Jacques, 2011; the presence or absence of a face identity effect in the right occipital inferior gyrus, see, e.g., Ramon, Dricot, & Rossion, 2010), which hinder our progress toward understanding the neural substrates of individual face perception. These discrepancies also make neural adaptation paradigms difficult to use in studies testing single neuropsychological cases, or with human populations with whom long duration experiments prove difficult and for which the signal-to-noise ratio of their data may not be very high (e.g., infants, small children, clinical populations).

Here we introduce a novel approach to non-invasively evaluate the sensitivity to facial identity in the human brain, which largely overcomes the above-mentioned limitations and which can potentially be applied to study multiple aspects of face perception in the human brain. This approach is based on the fact that repetitive stimulation of the human brain at a constant frequency (e.g., 8 cycles/s, or 8 Hz) leads to an electrical response that oscillates at the same frequency as the stimulus and that can be recorded from the scalp. This modulation of the electroencephalogram (EEG) was observed for the first time with visual stimulation (Regan, 1966) and named *steady-state visual-evoked potential* (SSVEP): a repetitive response whose constituent discrete frequency components—the stimulus fundamental frequency and its harmonics—remain constant in amplitude and phase over an extended period (Regan, 1966, 1989, 2009).

Like more classical transient visual ERPs, the SSVEP is thought to arise from the synchronous extracellular currents along the apical dendrites of pyramidal neurons in visual cortex (Nunez, 1981). Local field potential (LFP)
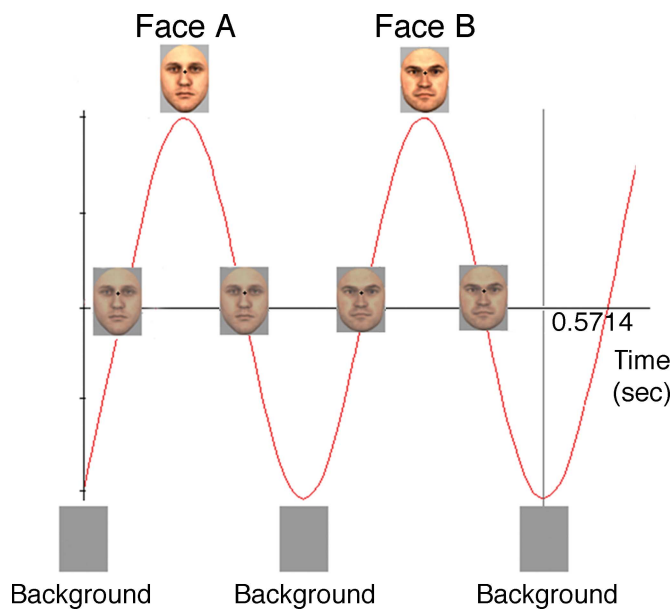
Figure 1. Stimulation used in this study (condition "different faces"). Full-front pictures of faces were presented at a rate of 3.5 cycles/s (3.5 Hz, one face every 285.7 ms, here two cycles presented), following a sinusoidal stimulation. The beginning of the 90-s stimulation (315 cycles in total, here 2 cycles represented) was always the (gray) background. The lower contrast face stimulus in the midline, in between the background and the full face stimulus, represents an intermediary stage of stimulation at the onset of the face stimulus. Hence, the total number of alternations between a face and the background was of 7 by second (7.0 Hz).

and multi-unit activity (MUA) recording studies of the cat visual cortex have shown that flicker stimuli of variable frequency evoked an oscillatory response with the same frequency as the stimulus rate in early visual areas (Rager & Singer, 1998; see also Krolak-Salmon et al., 2003 for LFP recordings at the monitor refresh rate frequency in the thalamus and human primary visual area). Neuroimaging (PET) studies have reported that changes in regional cerebral blood flow in the primary visual cortex follows an activation pattern similar to the SSVEP (i.e., maximal at about 15 Hz in this area for simple stimuli), indicating that the amplitude of the SSVEP corresponds to increased synaptic activity in visual cortex (Pastor, Artieda, Arbizu, Valencia, & Masdeu, 2003).

Compared to transient ERP methods, but also other neuroimaging methods, the main advantages of an SSVEP approach are its extremely high signal-to-noise ratio, its non-ambiguity with respect to the signal measured (at fundamental frequency f Hz, and harmonics $2f$ Hz, $3f$ Hz, …), and the ease with which it can be quantified (Regan, 1989). Thus, even if precise information about space and time is limited with this method, the advantages of SSVEPs make this a potentially highly useful method to investigate and characterize the sensitivity of the human brain to individual face perception.

SSVEP has been primarily used to study the brain's sensitivity to low-level properties of visual stimuli (contrast, phase, line orientation, spatial frequencies, motion, e.g., Ales & Norcia, 2009; Braddick, Wattam-Bell, & Atkinson, 1986; Campbell & Maffei, 1970; Heinrich & Bach, 2003; Tyler & Kaitz, 1977; see Regan, 1989), spatial and selective attention (e.g., Andersen, Müller, & Hillyard, 2009; Morgan, Hansen, & Hillyard, 1996), and figure–ground segregation (e.g., Appelbaum, Wade, Pettet, Vildavski, & Norcia, 2008; Appelbaum, Wade, Vildavski, Pettet, & Norcia, 2006). A few recent studies have also used SSVEPs with high-level visual stimuli and showed modulation of the SSVEP amplitude with the affective content of pictures (Keil et al., 2003), object familiarity (Kaspar, Hassler, Martens, Trujillo-Barreto, & Gruber, 2010), as well as to static and dynamic facial expressions (Mayes, Pipingas, Silberstein, & Johnston, 2009). However, to the best of our knowledge, none of these studies or other studies have attempted to use this method to address the issue of how (individual) faces are coded in the human brain.

Here we present the first study looking at the SSVEP response in the context of face identity repetition, in order to demonstrate the feasibility of the method and evaluate its potential to disclose sensitivity to high-level visual processes such as those used in face recognition. Twelve observers were presented with face stimuli alternating with a gray background 7 times/s (Figure 1). Thus, 3.5 face stimuli were displayed each second (fundamental frequency = 3.5 Hz), for a duration of 90 s. In one condition, the exact same face stimulus was presented consecutively (280 times/90 s; *identical face condition*), albeit at quite different sizes to minimize low-level adaptation. In a second condition, different face identities were presented successively (*different faces condition*). In line with the neuroimaging and electromagnetic studies mentioned above, we hypothesized that EEG power at 3.5 Hz would be much larger when different faces are presented than when the same face was repeated, with this difference being evident primarily over right occipito-temporal electrode sites. To ensure that any observed effects were not due to potential low-level adaptation, the exact same stimuli were also presented upside down, a manipulation that is known to greatly affect individualization of faces (Yin, 1969; for a recent review, see Rossion, 2009) and to reduce or abolish face identity adaptation in the right occipito-temporal cortex (Jacques et al., 2007; Mazard et al., 2006; Yovel & Kanwisher, 2005).

Materials and methods

Participants

Twelve healthy adult participants (right-handed, age range 18 to 26, 4 males) with normal or corrected vision

Figure 2. The two main conditions of the study, in which either the same face was repeated throughout the 90-s stimulation sequence (above), or different face identities were presented successively (below). Note that there were large changes of size between each face picture to minimize low-level adaptation effects. A fixation cross was also present on the top of the nose (not displayed here, see Figure 1).

took part in the SSVEP study for payment. One interest of the present study was to demonstrate the feasibility and practical application of the method, so that the duration of the SSVEP study was quite short (4 conditions × 90 s = 6 min + pauses). Therefore, following the SSVEP face stimulation, participants took part in other EEG experiments. Seven of the participants were tested a second time in the exact same SSVEP experiment (with order of conditions inverted for these participants), but the data were similar to the first test and not included in the present paper. Written informed consent was obtained from all participants prior to the experiment.

Stimuli

Ten full-front color pictures of faces were used (Figure 1). These pictures of faces were selected from a large database of laser-scanned faces (MPI), widely used in many previous studies of face processing (e.g., Leopold, Rhodes, Müller, & Jeffery, 2005; O'Toole et al., 1999). They were unfamiliar to the participants. The size of the basic set of faces was 4° × 5.73° of visual angle, but the face size increased or decreased at each presentation (see procedure below). All face stimuli were equalized in luminance. They were rotated 180° for the inverted conditions.

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 (Sim-Stim) running on Matlab (The Mathworks), on a light gray background. The stimulation was given as follows. In each condition, a face stimulus appeared and disappeared on the screen, with a rate of stimulation of 3.5 faces/s (one

face every 285.7 ms). The stimulation function was sinusoidal (rather than abrupt, as in a square wave function; Figure 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 (285.7 ms/2). 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, Figure 1). In the *identical face* condition, the same face, chosen randomly for each participant among the 10 face stimuli, was presented repeatedly. In the *different faces* condition, the 10 individual faces were used and presented in random order in the sequence (Figure 2). The only constraint was that the same face identity could not appear immediately after having been presented, so that the rate of face identity change was always 3.5 Hz. Note that in the *identical face* condition, the exact same picture was used rather than different pictures of the same person. This procedure was done first for practical reasons (i.e., difficulty of presenting 10 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 (N170), identical results were obtained whether different photographs of the same person (Jacques et al., 2007) or the exact same photograph (e.g., Caharel, Jiang et al., 2009; Jacques & Rossion, 2009; Kuefner, Jacques, Prieto, & Rossion, 2010) were used as adapter and target faces. Nevertheless, to minimize low-level (i.e., pixelwise) adaptation, the face stimulus changed in size with each presentation (random size between 82% and 118% of base face size), i.e., at a rate of 3.5 Hz, in all conditions. More importantly, the conditions *identical face* and *different faces* were also performed with the exact same set of faces turned upside down, so that there were 4 stimulation runs in total.

There was only one 90-s stimulation run for each of the 4 conditions. The order of conditions was counterbalanced across participants. The total duration of the experiment was 6 min of stimulation with a few additional minutes accumulated in short pauses between each experimental run. During each 90-s run, the participant was instructed to fixate a small black cross located centrally on the face, slightly below the bridge of the nose (Figure 1, see also Supplementary Figure S1). This fixation corresponds roughly to the optimal point for fast face identification (Hsiao & Cottrell, 2008; Orban de Xivry, Ramon, Lefèvre, & Rossion, 2008). The fixation cross changed color (red) briefly (200 ms) between 6 and 8 times during each run and the participant was instructed to detect the color changes by pressing a response key. This orthogonal task was used to maintain a constant level of attention from participants that was equal for all conditions of stimulation.

The choice of the 3.5-Hz stimulation frequency was made by considering several factors. First, we wanted to

avoid the lowest delta EEG frequency ranges (<2 Hz), which contain the largest part of EEG power (signal but also noise). However, we wanted to ensure that the fundamental frequency (3.5 Hz) and the second harmonic (7 Hz) would both fall below the EEG alpha range (8–12 Hz), which can greatly contaminate the signal with noise, particularly over posterior channels. Second, we chose a relatively slow frequency so that participants could very clearly perceive the differences between individual faces in the *different faces* condition. Finally, similar stimulation values (3.0 Hz–3.6 Hz) have been used successfully in recent studies investigating figure–ground segregation by means of SSVEP (e.g., Appelbaum et al., 2006). Note that contrary to a common assumption, the frequency of stimulation does not have to be high (>5 Hz) to elicit a reliable SSVEP response (Regan, 2009; Vialatte, Maurice, Dauwels, & Cichocki, 2009).

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 kΩ. EEG was digitalized at a 1000-Hz sampling rate and a digital anti-aliasing filter of 0.27 * sampling rate was applied at recording (at 1000-Hz sampling rate, the usable bandwidth is 0 to ~270 Hz).

EEG analysis

After a 0.5- to 100-Hz band-pass filter was applied, the EEG in each condition for each participant was re-referenced to a common average reference. A Fast Fourier Transform (FFT) algorithm was applied to a 60-s (210-cycle) window of stimulation starting 10 s after the beginning of stimulation. This was done to avoid contamination from transient responses triggered by the onset of the stimulation train and to allow some time for the system to be entrained by the stimulation (e.g., Chen, Seth, Gally, & Edelman, 2003; Srinivasan, Russell, Edelman, & Tononi, 1999). Given the long duration of analysis (60 s), the frequency resolution was very high (1000/6000 = 0.017 Hz). Hence, the frequency value of interest (EEG power at 3.5 Hz) was located within a very small frequency bin (0.017 Hz; Regan, 1989). EEG power (μV^2) at 3.5 Hz was extracted for each condition separately, for the whole set of channels from every participant. Signal-to-noise ratio (SNR) at each channel for this frequency was computed as the ratio of the power at the frequency of interest to the average power of the 20 neighboring bins (Srinivasan et al., 1999). Rather than considering a limited region of interest (i.e., posterior electrode sites) in this initial feasibility study, statistical comparisons between different and identical face conditions were made independently at each individual electrode site over the whole scalp using simple one-tailed *t*-tests (different faces − identical faces). To take into account the problem of multiple comparisons, differences were considered relevant if they concerned at least 3 contiguous channels associated with a *p*-value <0.05.

To obtain a more specific display of the face-related response at the fundamental frequency (3.5 Hz) on the main region of interest identified in the above FFT analysis (right occipito-temporal electrode sites), EEG data were also filtered using narrow band-pass filtering (3.0 Hz–4.0 Hz; 36 dB/octave; e.g., Toffanin, de Jong, Johnson, & Martens, 2009). Overlapping EEG epochs of 20 cycles (5714 ms), starting 30 cycles (8571 ms) after stimulation onset, were extracted and averaged (e.g., Müller et al., 2006). The zero time point of each epoch corresponded to the peak of gray background stimulation, i.e., when the face was not at all visible (Figure 1). There were a total of 315 EEG epochs averaged by participant by condition. The averaged waveforms were used to estimate the relative latency of the SSVEP response in each condition (first positive peak following stimulation).

Finally, to better characterize the evolution of the adaptation effects, we also performed distinct FFTs on 7 consecutive 12-s time windows, starting 2 s after the onset of stimulation (i.e., until 86 s) on electrodes of interest identified in the main FFT analysis (right occipito-temporal cluster). For each participant, EEG power was extracted for each condition (2) and time window (7) and analyzed using repeated measures ANOVAs.

Results

Participants were almost at ceiling for detection of color changes on the fixation cross (95.8–100%), without differences between conditions.

Upright faces: Adaptation effect

Following repetitive stimulation of *different* faces, there was a large peak of EEG power at the fundamental 3.5-Hz frequency over the whole scalp, with the largest activity being primarily located over lateral occipital and occipito-temporal channels (Figures 3 and 4). Average SNR over all channels at 3.5 Hz was of 15.41, with a maximum observed at a right occipito-parietal channel (POO4h,
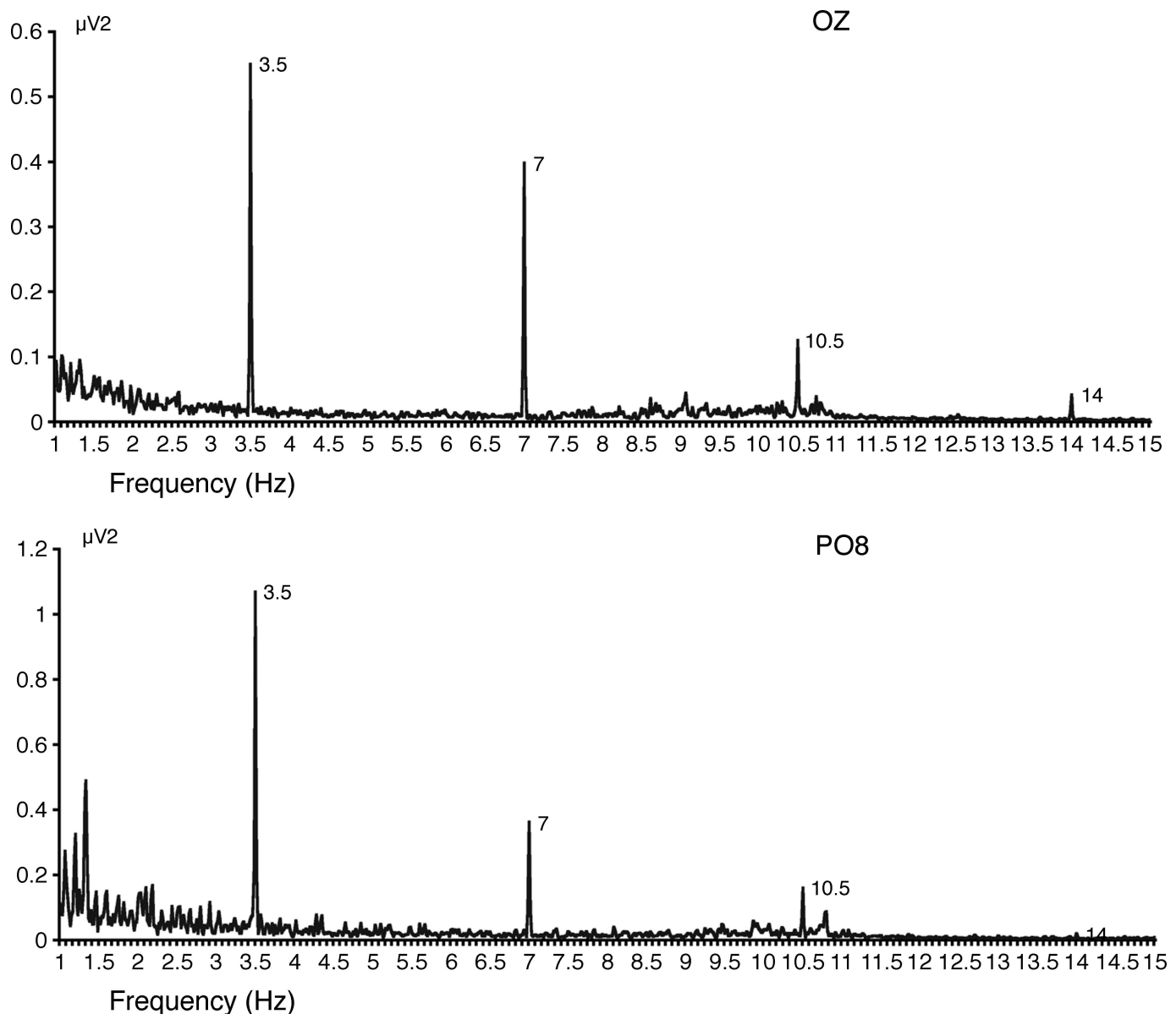
Figure 3. Averaged power spectra (1–15 Hz) of the 12 participants of the experiment in the "different faces" condition, displayed here for two occipital channels: OZ (central occipital) and PO8 (right lateral occipital). Note the large increases in power at the stimulation frequency (Fz, 3.5 Hz) and harmonics (2Fz, 3Fz, …). Power at these frequencies was the largest at right occipital lateral sites or occipito-temporal sites (e.g., PO8 > OZ).

SNR: 51.71) and an occipito-temporal channel (PO8, SNR: 48.19), and a minimum at a left prefrontal channel (FTT9h, SNR: 4.38).

There were also marked peaks from the second harmonic (7 Hz) to the 5th harmonic (17.5 Hz) although at much lower power values (Figure 3). However, the power and SNR decreased progressively with each harmonic from that of the fundamental frequency, and the scalp topography became less specific with each increasing harmonic. The behavior of the harmonics for which there were no consistent differences between conditions but a small advantage for different faces over identical faces only at 7 Hz (see Supplementary Figures S2–S6) was not analyzed further here and will be the subject of future investigations.

The same observations were made when the exact same face was presented throughout the sequence, that is, we observed a large peak of EEG power at 3.5 Hz mainly localized at posterior electrode sites (Figure 4). However, the power at 3.5 Hz was substantially smaller than for different faces, particularly over the right lateral occipital sites. Subtracting EEG power values obtained in this identical face condition from power values of the different faces condition revealed a well-focused difference on the scalp at bilateral occipito-temporal sites, with a clear right hemispheric dominance (Figures 4 and 5).
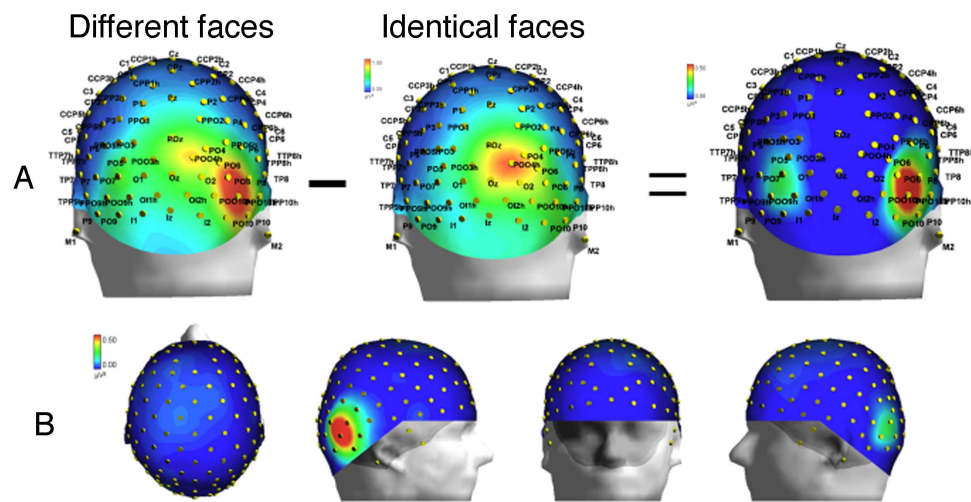
Figure 4. Topographical maps of EEG power at the fundamental 3.5-Hz frequency for the two conditions of interest. Power increase was the largest at posterior sites on the scalp in both conditions but with a peak at right lateral occipito-temporal sites only for different faces. Subtraction of the power for identical faces isolated the regions where different faces showed a specific increase of power relative to identical faces (for the sake of clarity, only positive differences are displayed on the figure).

Statistical comparison between the two conditions over all channels identified 7 contiguous channels on the right occipito-temporal scalp (PO8, P8, P6, PO10, PPO10h, POO10h, P10) showing a significantly larger power amplitude at 3.5 Hz for different than identical faces (*p*-values of the individual channels ranging between
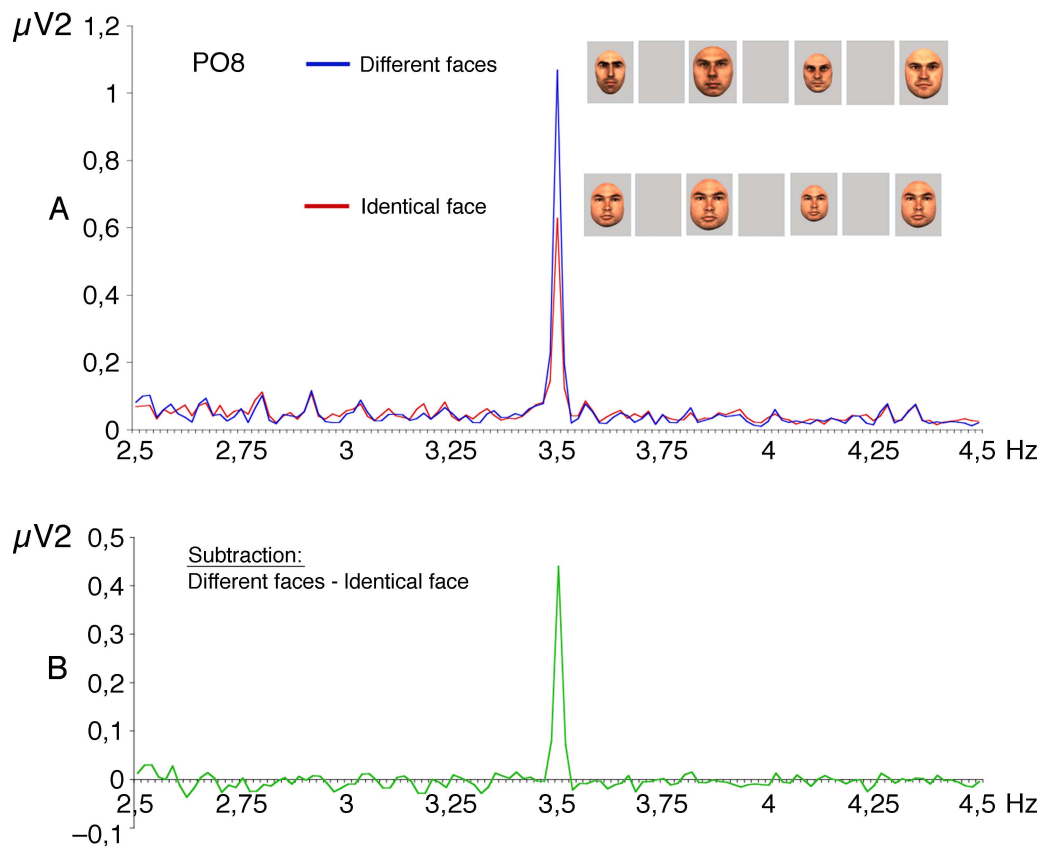

Figure 5. (A) Grand-averaged (*N* = 12 participants) EEG power at electrode PO8 between 2.5 and 4.5 Hz (centered on the fundamental frequency (3.5 Hz)), where different upright faces elicited a significantly larger response than identical upright faces. Note that the difference between the two conditions of interest arises only at the frequency of stimulation. (B) Subtraction between the two conditions (different faces − identical face).
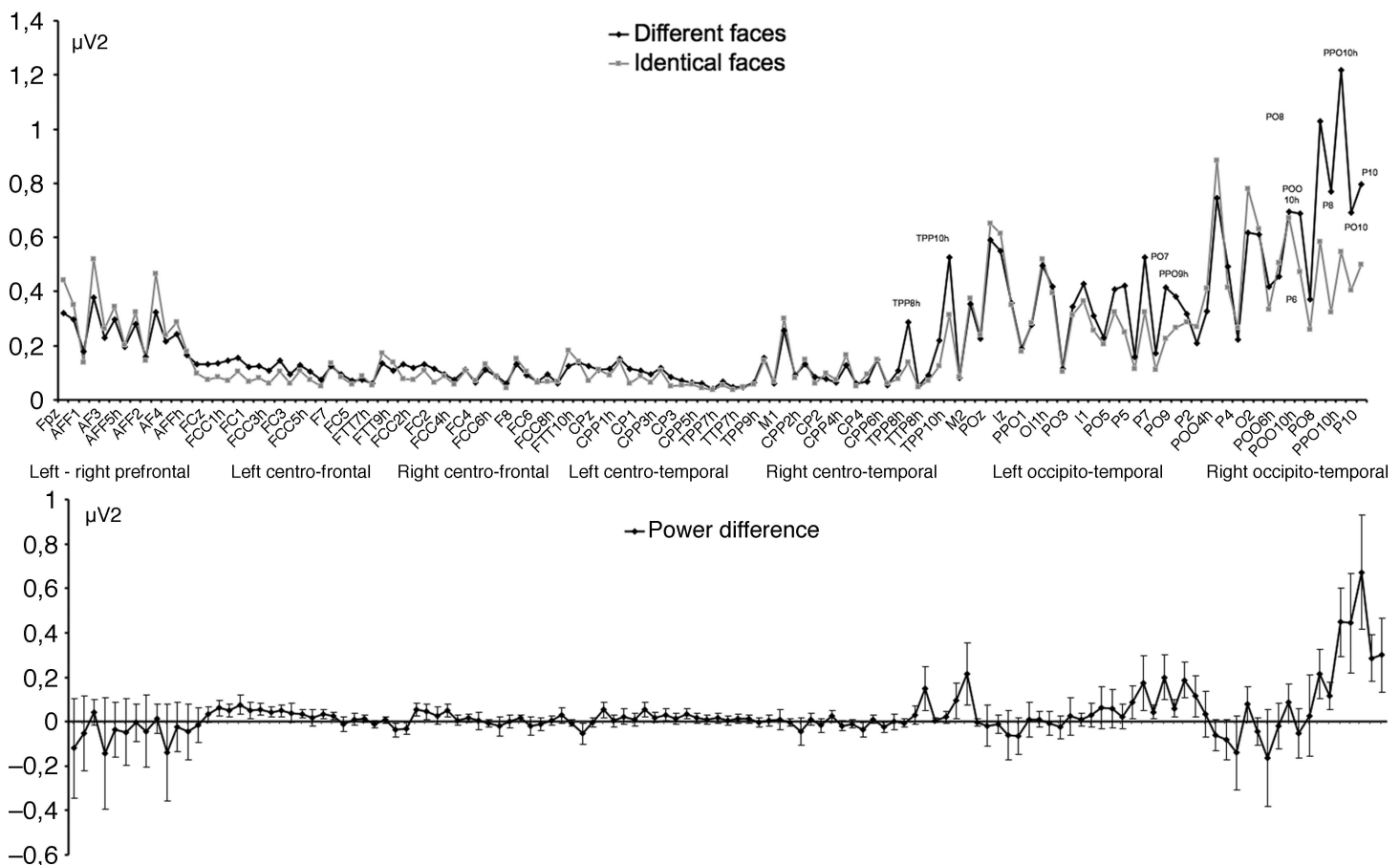
Figure 6. (Top) EEG power at each of the 128 electrode sites for the two conditions of interest (upright faces). There was a large increase of power at posterior electrode sites in the two conditions, with a large difference between the two conditions on right occipito-temporal sites (significant at the labeled electrodes), and to a much lesser extent at left occipito-temporal sites. (Bottom) Power difference between the two conditions ($\pm SE$ of the difference).

$p < 0.05$ and $p < 0.007$; Figure 6). There was also a region of 6 contiguous channels over left central electrodes in which overall power values were much smaller but significantly larger for different faces than identical faces (Figure 6; FC1, FC3, FCC3h, FFC2h, FFC1h, FFC3h; p-values between 0.03 and 0.05). There were no significant effects at any other channels over the whole scalp, with no channel showing a significantly larger response to identical than different faces (all other electrodes, $p > 0.06$), except for only two contiguous channels at occipito-temporal electrode sites over the left hemisphere (PPO9H, PO7, p-values = 0.02 and 0.04).

All channels that were close to a significantly larger response to different than same faces (15 channels between $p < 0.1$ and $p > 0.05$) were contiguous to the three areas identified.

Statistical analyses performed on SNR provided similar results, with a cluster of 8 contiguous electrodes at right occipito-temporal sites showing a significantly larger SNR for different faces than identical faces (PPO10h, P8, PO10, TPP8h, PO8, all $ps < 0.01$; P6, P10, TP8: $ps < 0.05$). There was also a 4-electrode cluster at homologous

left hemisphere sites (PPO9h, P7, P5, CPP5h, all $ps < 0.05$), but none of the left central electrodes, which showed that significant differences in the power analysis were significant using SNR values.

In summary, we observed much greater power at the frequency of interest (3.5 Hz) for different than identical faces, with significant differences focused mainly at right occipito-temporal electrode sites.

Inverted faces: (Lack of) adaptation effect

For inverted faces, in the condition *different faces,* a specific peak of EEG power was also found at 3.5 Hz (average SNR: 13.93, maximal SNR at PO6: 45.16; Figure 7A). Harmonics were also clearly visible from the peak at 7 Hz until the 5th harmonic (17.5 Hz). In contrast to upright faces, there were almost no visible differences in 3.5-Hz power at any channel when different faces were compared to identical faces (Figure 7A). Consequently, subtracting EEG power values obtained in the identical face condition from the different face condition did not
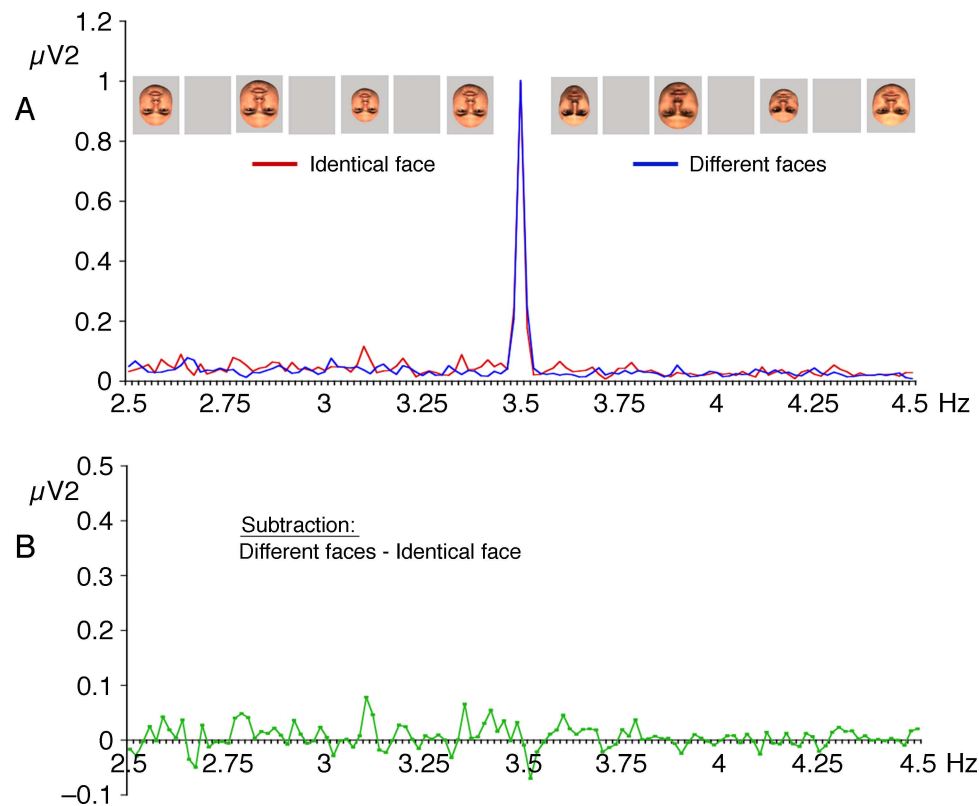
Figure 7. (A) Grand-averaged (*N* = 12 subjects) EEG power at electrode PO8 between 2.5 and 4.5 Hz (centered on the fundamental frequency (3.5 Hz)) for inverted faces. The response of interest was not larger for different faces than identical face presentation at the fundamental 3.5-Hz frequency, contrary to what was observed for upright faces (see Figure 5). (B) Subtraction between the two conditions for inverted faces. Contrary to upright faces, there was no larger response for different than identical faces.

reveal much difference (Figures 7B and 8). Statistical comparison based on EEG power between the two conditions over all channels revealed significant differences ($p < 0.05$) only for a group of 4 contiguous left parieto-central channels (CPP3h, P3, CPP1h, P1) showing a larger response to different faces than same faces ($p < 0.05$) and an isolated homologous channel in the right hemisphere (CP4). On two central occipital channels (Oi2h, Oi1h), a larger response to identical than different inverted faces was found (all other comparisons, $ps > 0.06$). On the exact same electrode sites where significant differences were found for upright faces over the right occipito-temporal cortex, *p*-values were all above >0.15 for inverted faces.

Statistical analyses performed on SNR showed only a cluster of 3 posterior electrodes in which there was a larger SNR for identical vs. different faces (O1, PO7, Ol1h: $ps < 0.05$).

Relative latency of SSVEP responses to faces

In summary, the clearest and most consistent pattern that we observed was a large increase of EEG power at the fundamental 3.5-Hz frequency for different as compared to identical upright faces, over right occipito-temporal sites. The larger response to different, compared to identical, upright faces, but not inverted faces, is clearly visible on averaged band-pass-filtered time windows displayed in Figure 9 for two typical participants. This analysis also shows that SSVEPs to different and identical faces are well phase-locked to stimulus onset for each individual subject and well in phase with each other. There were substantial variations of phase across participants (e.g., Figure 9) and a small advantage for identical faces in terms of relative latency (9 ms earlier, $t_{11} = 1.78$, $p = 0.05$, one-tailed) for upright faces only (-3 ms for inverted faces, $t_{11} = 0.46$, $p = 0.65$). Interestingly, inverted faces elicited delayed SSVEP compared to upright faces, ranging between 15 ms and 26 ms of latency delay (different faces: $t_{11} = 2.18$, $p < 0.05$; identical faces: $t_{11} = 5.05$, $p < 0.001$).

Characterization of adaptation effects: FFTs on consecutive time windows

FFTs on 7 consecutive 12-s time windows over the right occipito-temporal sites of interest showed that the difference observed between the two conditions for upright
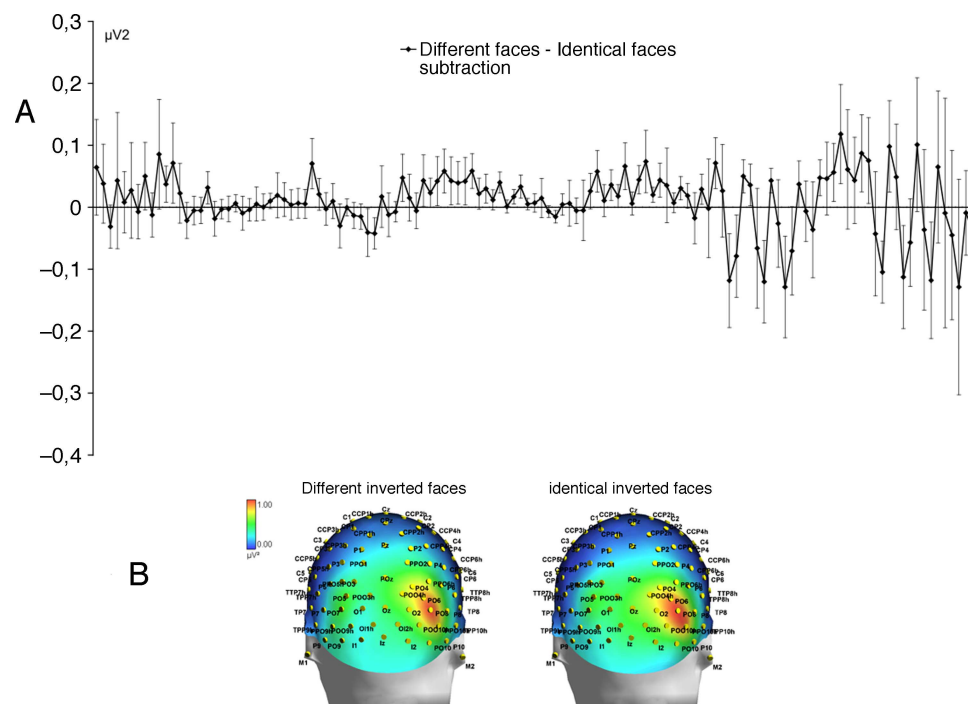
Figure 8. (A) EEG power difference between the two conditions (±*SE* of the difference) across all channels for inverted faces (compare to Figure 6 for upright faces). (B) Topographical maps of identical and different faces, showing that the right occipito-temporal response was roughly of equivalent magnitude in the two conditions for inverted faces.

faces was due to a decrease of amplitude for identical faces over time (Figure 10). There was a significant decrease of signal over time for identical faces (ANOVA$_{Rm}$, main effect of time windows, $F_{6,66} = 3.51$, $p = 0.0045$) but not for different faces ($F_{6,66} = 0.53$, $p = 0.77$).

Discussion

SSVEP evidence for sensitivity to individual faces in the right occipito-temporal cortex

Presentation of face photographs at the fixed rate of 3.5/s led to a large electrical response oscillating at that specific frequency, with a posterior distribution on the scalp covering the whole visual cortex. When the exact same face identity was repeated—albeit with substantial changes in retinal size stimulation—the oscillation at the fundamental 3.5-Hz frequency was much smaller in amplitude as compared to when different faces were presented at the same rate. This larger amplitude for different, compared to identical, faces was localized over lateral occipito-temporal sites, particularly in the right hemisphere.

This novel observation can be taken as another marker of the human brain's sensitivity to individual faces, observed at a global scale. These findings are in agreement with fMRI studies reviewed in the Introduction

section, which shows larger neural responses to the abrupt onset presentation of pairs, or trains, of different faces as compared to identical faces in several face-sensitive areas of the occipito-temporal cortex (e.g., Andrews & Ewbank, 2004; Gauthier et al., 2000; Gilaie-Dotan & Malach, 2007; Grill-Spector & Malach, 2001; Schiltz et al., 2006; Winston et al., 2004; Yovel & Kanwisher, 2005). Electromagnetic studies have also reported a larger N170/M170 amplitude when different faces are presented consecutively as compared to the presentation of the same face, with such effects being prolonged until about 300 ms following stimulus onset (Caharel, d'Arripe et al., 2009; Caharel, Jiang et al., 2009; Ewbank et al., 2008; Heisz et al., 2006; Itier & Taylor, 2002; Jacques et al., 2007; for a review, see Rossion & Jacques, 2011).

When considering occipito-temporal sites, the scalp topography of the two conditions of the present study (identical and different faces) showed a right hemisphere advantage (Figure 4). The larger response in the right hemisphere in both conditions is in agreement with the well-known right hemispheric dominance for unfamiliar face perception. Acquired prosopagnosia follows either bilateral or right unilateral occipito-temporal lesions (Bouvier & Engel, 2006; Hecaen & Anguelergues, 1962), and multiple sources of evidence ranging from divided visual field studies (Hillger & Koenig, 1991; Parkin & Williamson, 1987), neuroimaging (e.g., Kanwisher et al., 1997; Sergent et al., 1992), transient ERPs (N170; Bentin, McCarthy, Perez, Puce, & Allison, 1996) to single-cell recordings in the non-human primate brain (Perrett et al.,
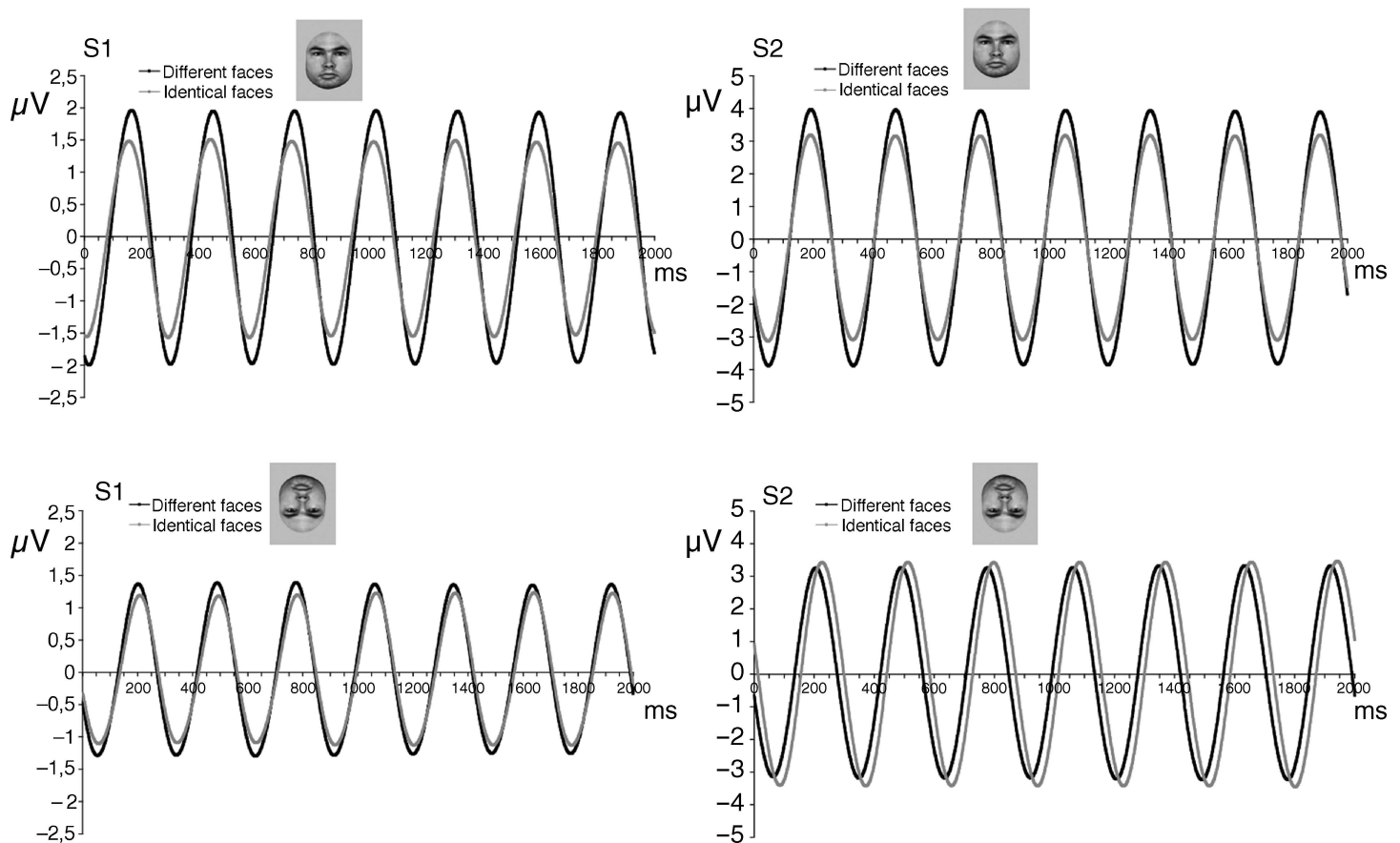
Figure 9. Averaged waveforms time-locked to the gray background stimulation, for different and identical faces, in two typical subjects of this experiment. For each subject, the right occipito-temporal electrode showing the largest signal over the two conditions is displayed, P10 for S1 and PO8 for S2. (Top) Upright faces. (Bottom) Inverted faces. The waveforms were obtained by narrowband filtering the EEG signal (3–4 Hz) and computing averages over overlapping windows of 30 cycles time-locked to stimulus onset (gray background). There is a much larger response to different than identical upright faces but not for inverted faces. Note that the two conditions (different and identical) are well in phase with each other, at each orientation. However, there is a significant delay of the SSVEP response to inverted as compared to upright faces (see Supplementary Figure S7).

1988) have supported the dominant role of the right posterior visual areas in processing faces.

This lateralization was even more pronounced when the two conditions of the present study were contrasted, isolating the effect of face identity repetition on a few contiguous right occipito-temporal channels. This dominant right hemisphere posterior scalp topography is also in agreement with the observations of generally larger fMRI face adaptation effects in the right vs. left hemisphere face-sensitive occipito-temporal areas (e.g., Gilaie-Dotan & Malach, 2007; Schiltz & Rossion, 2006). More strikingly, the spatial distribution and the right hemispheric advantage of the effect observed in the present study is remarkably similar to the scalp topography obtained for the differential N170 response observed for a face preceded by a different as compared to an identical face in a transient ERP paradigm (Jacques et al., 2007; see Caharel, d'Arripe et al., 2009; Caharel, Jiang et al., 2009; Kuefner, de Heering, Jacques, Palmero-Soler, & Rossion, 2010 for data acquired with the exact same recording

system as in the present study). This observation suggests that the SSVEP paradigm as used here measured the same phenomenon, at least in large part, as observed in previous face identity adaptation ERP studies using transient stimulation.

Importantly, despite using the same face photograph in the "identical face" condition, the smaller SSVEP response at the fundamental frequency in this condition compared to different faces cannot be accounted for by an effect of repetition of low-level visual features (in the identical face condition), for several reasons. First, the effect was observed despite substantial changes of stimulus size (up to 40%), excluding the possibility of pixelwise repetition effects. Second, rather than being widespread, the effect was found at a specific frequency value, the fundamental frequency of stimulation (3.5 Hz). Third, the lateralization and localization of the effect on the scalp clearly suggests that it concerns high-level rather than low-level visual areas. Finally, we did not find any differences between conditions for the exact same stimuli
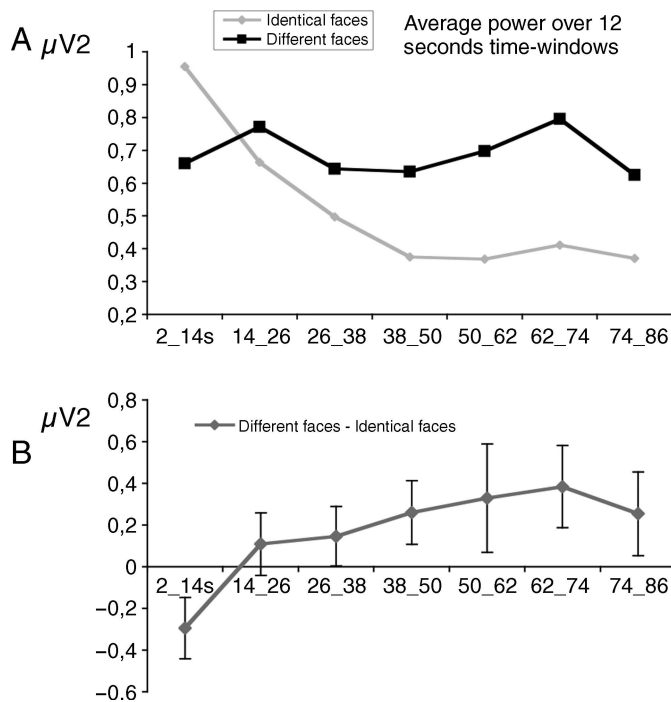
Figure 10. (A) Grand-averaged power values computed over 12-s time windows on a region of interest over the right occipito-temporal hemisphere. The seven channels where significant power differences were found are averaged for the two conditions of interest (upright faces). The windows of analysis start 2 s after onset of visual stimulation. Note that power was larger for identical than different faces at the beginning of stimulation (window 2 to 14 s) but decreased steadily for identical faces until it reached a plateau after a few tens of seconds. In contrast, EEG amplitude remained somewhat constant when different faces were presented along the sequence. (B) Power difference between the two conditions ($\pm SE$ of the difference) over each time window of stimulation.

when they were presented upside down, despite the fact that the inverted faces elicited a large SSVEP response.

Advantages of the approach

With respect to previous studies, the present observations go beyond providing further evidence for the neural representation of individual faces in the human brain, in particular in the right occipito-temporal cortex. The approach introduced here highlights the many advantages of the SSVEP method (Regan, 1989), supporting the idea that it can be an excellent tool to investigate the neural coding of individual faces and high-level visual representations in general. First, in contrast to fMRI and transient ERP/ERMf studies, for which the definition of areas and components/time windows of interest can be quite subjective and differ between studies, here there is no ambiguity in selecting the component of interest. That is, one can focus on EEG power at the precise frequency at

which faces alternated with each other (3.5 Hz here). The measurement is highly selective, as potential differences between the two conditions in other frequency ranges do not contaminate the measurement and could easily be controlled for if needed (SNR computation). Second, whereas in transient ERP studies measuring the amplitude of a target potential can be an issue (e.g., peak maximum or average amplitude in a time window, problem of local maxima/minima, baseline to peak or peak-to-peak measures, see Handy, 2004; Luck, 2005), here the response and the difference between conditions can easily be quantified. Third, and most importantly, the SNR of the response of interest is quite impressive, being much larger with this SSVEP approach than with other methods that require the registration of many trials to produce signal with a good SNR, and thus experiments of much longer duration. One reason for the high SNR of the SSVEP is that spontaneous EEG fluctuations and artifacts, such as alpha waves, blinks, and muscle potentials, tend to take place in certain frequency ranges that can be avoided by the choice of the target frequency. For instance, here the 3.5 Hz (and the second harmonic at 7 Hz) fall in between the lowest frequency bands carrying a large part of the EEG power spectrum (lower delta, <2 Hz) and the spontaneous waves of the alpha range (8–12 Hz). In contrast, the N170 face-sensitive component of interest in transient ERP studies corresponds to a time- and phase-locked increase of EEG power falling mainly within the alpha range (5–15 Hz; Rousselet, Husk, Bennett, & Sekuler, 2007; see also Klopp, Halgren, Marinkovic, & Nenov, 1999), making great reductions in SNR possible. Moreover, while spontaneous EEG fluctuations and artifacts have broad-band spectra in these frequency ranges, here the frequency resolution of the FFT is particularly high, and the response can be identified in a very narrow frequency band (0.017 Hz). Thus, the SSVEP approach can have immense practical value in segregating stimulus-related brain activity from both artifacts and spontaneous brain activity (Regan, 1989; Srinivasan, Bibi, & Nunez, 2006). Finally, probably for the reasons just mentioned, the difference found between the two conditions of upright faces was extremely large (about a 50% increase of EEG power on average at right occipito-temporal electrode sites) for an experiment that lasted only a few minutes (90 s of testing by participant/condition).

Practical interests and potential applications

The method introduced here is thus quite powerful and sensitive, to a level that, in our experience, is unparalleled by any of the other methods used to test the sensitivity to individual face perception in the human brain. Considering these advantages, it could be particularly valuable to test the sensitivity to face individualization in human populations who can be tested only for short durations and/or who present a lower SNR in their EEG, such as

infants, small children, or brain-damaged patients. For instance, performance in face individualization improves greatly between 4 years and adulthood (e.g., Carey & Diamond, 1977; Chung & Thomson, 1995; Mondloch, Le Grand, & Maurer, 2002). However, whether this improvement reflects an increased sensitivity of perceptual face processing remains unclear (Crookes & McKone, 2009) because behavioral performance can be affected by many general functions that are known to develop until adolescence. While there is evidence that the sensitivity to faces (with respect to other visual categories) of the N170 found at age 4 (Taylor, McCarthy, Saliba, & Degiovanni, 1999) does not vary throughout development (Kuefner, de Heering et al., 2010), its susceptibility to individual faces has not been tested in children. Testing this would be a challenge because sensitive N170 adaptation paradigms require long duration experiments to obtain a reliable effect (e.g., Jacques et al., 2007). In contrast, sensitivity to different individual faces could potentially be tested with the SSVEP approach introduced here, under the exact same conditions between infancy and adulthood.

In addition, given that the component of interest can be identified unambiguously in different population of participants, the magnitude of the sensitivity to individual faces could be more easily and directly compared across age groups with such an SSVEP approach than with a classical transient visual EP approach. For instance, the relationship between face-sensitive ERPs observed in infants and adults remains unclear, with two relatively late infant components, the N290 and P400, having been identified as potential precursors of the adult N170 based on their response properties (de Haan, Johnson, & Halit, 2003). However, this relationship remains highly speculative. With an SSVEP paradigm, such as that introduced here, one could directly compare the differential EEG power obtained for trains of different and identical faces at the exact same target frequency across age groups, so that there would be no ambiguity in the selection of the component of interest.

Finally, the power of the approach used here could be invaluable to testing the sensitivity to more subtle variations between features defining face identity. For instance, one could compare the presentation of identical faces to the presentation of faces varying only in terms of surface (color, texture) cues or to shape cues only (Caharel, Jiang et al., 2009). The contribution of specific features (e.g., eyes or mouth, inter-distance relationships…) that differ between faces to face individualization could also be investigated with a greater chance of success than in studies relying on less sensitive methods.

Caveats and limitations

Admittedly, the SSVEP approach, as introduced here to investigate face individualization, also has its limitations

or uncertainties, and the parameters selected for a given experiment may affect the observations made.

Spatial resolution

Spatial resolution of the EEG (and MEG) is limited, whether one measures transient or steady-state ERPs: there will always be a substantial degree of uncertainty about the exact localization of the neural sources generating the component of interest recorded on the scalp (Helmholtz, 1853; Snyder, 1991). However, we note that while the basic response at the fundamental frequency (3.5 Hz) was widespread over the back of the brain here, as in previous SSVEP studies (e.g., Appelbaum et al., 2006; Di Russo, Martýnez, Sereno, Pitzalis, & Hillyard, 2002; Herrmann, 2001; Pastor et al., 2003; Srinivasan et al., 2006), the *difference* between the two conditions was surprisingly quite focal in terms of its topography, being well localized over right occipito-temporal sites (Figure 4). As noted above, this localization is perfectly congruent with previous ERP evidence and with the known localization of face adaptation effects in areas identified by fMRI, indicating that spatial localization of the SSVEP effects can be quite informative about the potential neural sources generating such effects. Moreover, the very high SNR of this method may also be an advantage when applying inverse source localization methods to model the spatial distribution of neural activity underlying the scalp EEG signals (see, e.g., Appelbaum et al., 2006; Di Russo et al., 2007; Van Dijk & Spekreijse, 1990).

Temporal resolution

Transient ERP studies allow a chronometric analysis of successively evoked brain activity and have been particularly informative about the time course of face categorization and of face individualization in particular (Rossion & Jacques, 2011). In contrast, an intrinsic disadvantage of SSVEP is that the rapid visual stimulation does not allow brain activity to return to a baseline state before the next stimulus appears, thus making it unable to directly derive time information from the SSVEP. However, using multiple frequencies of stimulation, the SSVEP latency can be somewhat estimated from the slope of the regression line of VEP phases as a function of temporal frequency ("apparent latency", Di Russo et al., 2002; Regan, 1966, 1989; Spekreijse, Estevez, & Reits, 1977). More simply, the delay between the visual stimulus and the waveform at a given fundamental frequency, i.e., the phase, can be extracted from the FFT, even though it is difficult to infer the absolute time course of the effects of interest from such phase values. Yet, relative latency differences between conditions or between areas of interest where neural activity is modeled (Appelbaum et al., 2006) can be inferred by taking into account the phase of the waveform at the fundamental frequency. For instance,

here, interestingly, despite a substantial amount of variability across individuals in terms of the phase of the waveform at fundamental frequency, there was a systematic and significant phase delay between the presentation of upright and inverted faces, of about 15 ms–25 ms, on the right occipito-temporal electrodes of interest. This observation is in line with latency delays observed in the response to inverted with respect to upright faces in single neurons of IT in the monkey brain (Perrett et al., 1988) and on the human N170 face-sensitive component (Bentin et al., 1996; Rossion et al., 1999), although the time delay appears to be slightly larger in magnitude here. Thus, while this issue of relative latency differences between conditions of face stimulation should be more thoroughly addressed in future studies, this observation suggests that face-related SSVEP may be informative about the relative timing of neural activation to faces and other visual stimuli.

Block design and potential effects of attention

Another limitation of the present approach is that it requires a block design, in which blocks of different and identical faces are compared, and a constant rate of stimulation. This mode of stimulation is not ideal because differences between conditions could possibly arise due to participants' fatigue or boredom following the presentation of the exact same event or to expectations and anticipations about the nature of the stimuli presented. Moreover, many studies have shown that SSVEP amplitude is highly sensitive to attention, with increases in amplitude occurring when observers pay attention to a specific stimulus (e.g., Di Russo et al., 2002; Morgan et al., 1996; Müller et al., 2006; Toffanin et al., 2009), or even decreases that occur when attention is not focused on the visual stimulus (Chen et al., 2003). Note that a general factor such as selective attention is unlikely to account for the present observations, for several reasons. First, we used an orthogonal task, which had nothing to do with the differences between conditions, which was performed equally well for each condition. Second, the effect observed was not widespread but rather very focal, taking place on electrode sites located over cortical regions known to be particularly involved in face perception, and where early (160 ms) transient ERP face identity adaptation effects are observed in event-related paradigms (Jacques et al., 2007). Third and most importantly, the effect was found only for upright faces but not when an identical face was presented upside down.

In future studies, in order to minimize the influence of attentional factors, and yet maintain the advantages of the SSVEP approach, one could perhaps use a stimulation mode in which a sequence of identical face stimuli at frequency F1 would be interrupted with a rare stimulus (different face) at regular intervals (e.g., F1/7 = F2). FFT of the EEG signal should then reveal a peak at F2 that could be related to the differential process between individual faces (see Heinrich, Mell, & Bach, 2009).

Frequency of stimulation

Here, for various methodological reasons already mentioned, a relatively slow frequency of stimulation was selected (3.5 Hz), giving rise to large SSVEP and differences between the two conditions of interest. However, SSVEP amplitude can be greatly affected by flicker frequency (e.g., Herrmann, 2001; Regan, 1966, 1989; Srinivasan et al., 2006; van der Tweel & Verduyn Lunel, 1965) and there may be major differences in the properties of electrical responses at different frequencies to sinusoidally modulated light (Regan, 1989). Moreover, attentional effects on SSVEP also vary depending on the frequency of stimulation (e.g., Ding, Sperling, & Srinivasan, 2006). Therefore, even though time-locked decreases of EEG signal following object repetition have been observed in high-frequency ranges (Gruber & Muller, 2005), it is unlikely that the effects observed here would be found at all frequencies that have been shown to elicit reliable SSVEP (e.g., until 90 Hz in Herrmann, 2001) and would be of comparable magnitude across various frequency ranges. Rather, it is likely that the technique can be further refined and that the effects observed here could even be stronger at different frequency ranges. Hence, determining the optimal frequency ranges for perception of individual faces with a similar approach to that used here may have further theoretical and practical implications.

Inter-subject variability in SSVEP power

As in previous studies, EEG power was quite variable across individual participants at the frequency of interest, ranging for instance between 0.08 μV^2 and 3.8 μV^2 at a right lateral occipital electrode of interest (PO8) in the same condition. SNR measures were at least as variable across participants, with values ranging from less than 2 (twice the power in the frequency bin of interest than in neighboring bins) to more than 100 for the same electrode in the same condition. This variability across participants in terms of magnitude of the response and of the magnitude of the difference between conditions appears to be higher than for other measures such as face-sensitive transient ERPs. Multiple repetitions of each stimulation run of each condition for each participant could help reduce this variance but at the expense of longer duration experiments. In any case, this variance is a factor that should be considered when comparing different populations, preferably across conditions.

Unknown underlying mechanisms of SSVEP adaptation

We observed that the large and specific EEG response at the frequency of stimulation remained stable when different face identities were presented but decreased over time when the exact same facial identity was repeated. As

mentioned above, this latter phenomenon can be related to the adaptation effect observed for the consecutive presentation of identical faces in the occipito-temporal cortex, with a right hemisphere advantage. However, given that a definition of the SSVEP is that the response remains constant in amplitude over an extended period (Regan, 1966, 1989, 2009), "adaptation of SSVEP" is a contradiction of terms, and one should remain careful with the exact terminology until the neural mechanisms of this phenomenon are better understood. Even though SSVEPs have been described as being largely immune to habituation (e.g., Heinrich et al., 2009; Regan, 1989), studies using low-level visual stimuli (e.g., checkerboards, gratings) have shown SSVEP amplitude decreases following the prolonged (tens of seconds) repetition of the same pattern reversal (Heinrich & Bach, 2001; Peachey, DeMarco, Ubilluz, & Yee, 1994). However, these studies did not only differ from the present one with respect to the kind of stimuli used (i.e., low-level vs. a multi-dimensional complex pattern belonging to a familiar category here), but they did not compare the condition involving the repetition of the exact same stimulus to a condition in which different stimuli of the same kind (category) are presented at the same frequency. Therefore, one could not exclude that the adaptation effects reported in such studies might have been due to general attentional and fatigue factors.

In addition, low-level SSVEP adaptation effects were reported in these studies only for one or a few scalp electrodes only, so that their specificity to the type of stimulation used is difficult to assess. Here because of the high-density recordings used, the data revealed adaptation effects having a quite specific scalp distribution over the right lateral occipito-temporal sites. As mentioned above, this scalp distribution is highly similar to the neural adaptation effects measured by transient ERP responses (Caharel, d'Arripe et al., 2009; Caharel, Jiang et al., 2009; Jacques et al., 2007; Kuefner, Jacques et al., 2010), suggesting that their neural basis might be identical.

Regarding the time course of the effect disclosed here, there are also similarities with neural adaptation effects as reported in the BOLD signal in fMRI and action potentials in single-cell recordings. For instance, repetition suppression increases with more repetitions of the same stimulus, such that firing rates or BOLD responses resemble a negative (decreasing) logarithmic function of presentation number, often reaching an asymptote (Grill-Spector & Malach, 2001; Li et al., 1993; Müller, Metha, Krauskopf, & Lennie, 1999; see Figure 9). Moreover, and interestingly, we also observed a larger initial response of the SSVEP when identical faces were presented, relative to different faces. Such large initial responses followed by large decreases with repetitions of visual objects have also been observed in the low-level SSVEP studies mentioned above (Heinrich & Bach, 2001; Peachey et al., 1994) and in fMRI for more complex stimuli (James, Humphrey, Gati, Menon, & Goodale, 2000). Single-cell recording

studies have also shown that the adaptation of the neurons' response is usually delayed with respect to the initial visual response (see Ringo, 1996). Here, it may well be that in face-sensitive regions the initial buildup of the oscillation at the specific frequency f Hz is facilitated by the presentation of identical (size-invariant) stimuli as compared to the presentation of different face identities. However, after this initial synchronization with the stimulus, adaptation of the 3.5-Hz oscillation takes place when the identical face is repeated. Likewise, in keeping with the characteristics of neural adaptation effects described previously, we observed a slightly earlier latency of the response when identical upright faces were presented as compared to different faces, an effect that has been reported previously over similar scalp locations in an MEG adaptation study using shapes defined by random blinking dots (Noguchi, Inui, & Kakigi, 2004).

Admittedly, the goal of the present study is not to clarify all of these issues but to report a new phenomenon with the potential of being particularly useful and informative about the processes of face individualization in the human brain. More generally, the neural mechanisms of the effect observed here remain unclear and may correspond to any of the models that have been proposed to account for neural adaptation effects: (1) fatigue of the neurons responding to the stimulus; (2) sharpening of the representation, with fewer neurons being involved in coding the repeated face; or (3) facilitation of the representation with a reduction of processing time (Grill-Spector et al., 2006). Coupling single-cell recordings in face-sensitive areas defined by fMRI in the monkey brain (e.g., Tsao, Freiwald, Tootell, & Livingstone, 2006) with such stimulation paradigms should greatly enhance our understanding of the underlying neural mechanisms of this phenomenon.

Upright vs. Inverted faces and lack of adaptation effect for inverted faces

When faces were presented upside down, the larger SSVEP amplitude for different than identical faces disappeared completely. This absence of effect for inverted faces cannot be attributed to a small overall SSVEP response, or SNR, to inverted stimuli (Figure 7). This absence of effect for inverted faces is consistent with the observation that inversion substantially reduces discrimination and recognition for individual faces (e.g., Yin, 1969; for a recent review, see Rossion, 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 & Kanwisher, 2005). Similarly, the N170 face-identity adaptation 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

adaptation effects for inverted than upright faces have also been observed in face-sensitive areas in other fMRI studies (Gilaie-Dotan, Gelbard-Sagiv, & Malach, 2010; Goffaux, Rossion, Sorger, Schiltz, Goebel, 2009). Moreover, adaptation effects for inverted faces are also found over right occipito-temporal leads—at a weaker magnitude—after the N170 component (~210 ms, Jacques et al., 2007). Hence, one cannot exclude that in an SSVEP paradigm, by changing stimulation parameters, for instance the frequency of stimulation, identity adaptation effects could also be found for inverted faces. Yet, such effects should probably be of smaller magnitude than for upright faces.

Finally, it remains unclear whether the large repetition suppression effect observed in the present study when identical stimuli are presented at a fixed rate is specific to the face category. In fact, the method could—and should—be used with exemplars from other visual object categories and would probably lead to similar repetition suppression effects. However, humans are particularly good at individualizing faces, especially when one considers the visual homogeneity of the category, and the effects might be particularly salient with such stimuli. Moreover, it is known that individualization of faces relies specifically or to a greater extent on holistic/configural representations than other object categories (e.g., Biederman & Kalocsai, 1997; Farah, Wilson, Drain, & Tanaka, 1998). In this respect, the fact that the effect reported here was present mainly on the right hemisphere and was not found for inverted faces suggests that it is probably related to individualization of faces based on holistic/configural representations, a topic of interest for future research with this methodology.

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