



An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation



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ABSTRACT

We introduce an approach based on fast periodic oddball stimulation that provides objective, high signal-to-noise ratio (SNR), and behavior-free measures of the human brain's discriminative response to complex visual patterns. High-density electroencephalogram (EEG) was recorded for human observers presented with 60 s sequences containing a base-face (A) sinusoidally contrast-modulated at a frequency of 5.88 Hz (F), with face size varying every cycle. Different oddball-faces (B, C, D...) were introduced at fixed intervals (every 4 stimuli = $F/5 = 1.18$ Hz: AAAABAAAACAAAAD...). Individual face discrimination was indexed by responses at this 1.18 Hz oddball frequency. Following only 4 min of recording, significant responses emerged at exactly 1.18 Hz and its harmonics (e.g., $2F/5 = 2.35$ Hz, $3F/5 = 3.53$ Hz...), with up to a 300% signal increase over the right occipito-temporal cortex. This response was present in all participants, for both color and greyscale faces, providing a robust implicit neural measure of individual face discrimination. Face inversion or contrast-reversal did not affect the basic 5.88 Hz periodic response over medial occipital channels. However, these manipulations substantially reduced the 1.18 Hz oddball discrimination response over the right occipito-temporal region, indicating that this response reflects high-level processes that are partly face-specific. These observations indicate that fast periodic oddball stimulation can be used to rapidly and objectively characterize the discrimination of visual patterns and may become invaluable in characterizing this process in typical adult, developmental, and neuropsychological patient populations.

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1. Introduction

One of the most fundamental and complex functions of the human brain is to discriminate between visually similar items in order to guide behavior. Our ability to differentiate people based on their faces illustrates the potential finesse of such discrimination. Despite the high similarity between faces, humans are extremely efficient at accomplishing this task. Behavioral studies have revealed which visual cues play an important role in individual face discrimination. For instance, the eye region is particularly diagnostic (Haig, 1985; Sadr, Jarudi, & Sinha, 2003), and at the global level of the face, shape and surface cues (e.g., texture, color) provide complementary information (Jiang, Blanz, & O'Toole, 2006; see Bruce & Young, 2012). Furthermore, there is evidence that facial features are not processed independently, but integrated into so-called "holistic/configural" representations, which facilitate individual face discrimination (Sergent, 1984;

Young, Hellawell, & Hay, 1987; Tanaka & Farah, 1993; Farah, Wilson, Drain, & Tanaka, 1998; Rossion, 2013). At the neural level, there is an entire neural network involved in individual face discrimination, with key areas located in the right ventral occipito-temporal cortex (Sergent, Ohta, & MacDonald, 1992; Gauthier et al., 2000; Grill-Spector et al., 1999; Andrews & Ewbank, 2004; Schiltz & Rossion, 2006; Gilae-Dotan & Malach, 2007; Davies-Thompson, Gouws, & Andrews, 2009; Xu & Biederman, 2010).

The true complexity of face discrimination is highlighted by the considerable inter-individual variance of this ability in the normal adult population (Bowles et al., 2009; Wilmer et al., 2010). Long-term deficits, in the absence of brain damage, seem to be more prevalent than initially thought (Behrmann & Avidan, 2005; Duchaine & Nakayama, 2006). Additionally, this function can be impaired by simple stimulus manipulations such as picture-plane inversion or contrast-reversal. These two manipulations dramatically reduce individual face discrimination performance (for inversion, see e.g., Yin, 1969; Freire, Lee, & Symons, 2000; for a review, see Rossion, 2009; for contrast-reversal, see e.g., Galper, 1970; Bruce & Langton, 1994; Russell, Sinha, Biederman, & Nederhouser,

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2006; Russell, Biederman, Nederhouser, & Sinha, 2007). Humans are also poor at discriminating individual faces of a non-experienced morphology (e.g., the “other-race effect”, Malpass & Kravitz, 1969; for review: Rossion & Michel, 2011, and the “other-age effect”, Kuefner, Macchi Cassia, Picozzi, & Bricolo, 2008; Hills & Lewis, 2011; for a review: Rhodes & Anastasi, 2012). Individual face discrimination may be further impaired in neuropsychiatric disorders such as autism (Boucher & Lewis, 1992; Klin et al., 1999), or in the right variant of fronto-temporal dementia (e.g. Gainotti, Barbier, & Marra, 2003). In case of brain damage to right occipito-temporal areas leading to prosopagnosia, individual face discrimination can be severely and specifically disrupted (e.g., Hécaen & Angelergues, 1962; Barton, Cherkasova, Press, Intriligator, & O'Connor, 2004; Bouvier & Engel, 2006; Busigny, Graf, Mayer, & Rossion, 2010).

The importance of understanding individual face discrimination calls for an objective and highly sensitive discrimination measure, which could be recorded independently from behavioral performance and without contamination by irrelevant attentional and decisional processes. Such an approach was recently proposed in the form of electrophysiological (electroencephalogram, EEG) recordings on the scalp during fast periodic visual stimulation (e.g., Rossion & Boremanse, 2011), which results in steady-state visual evoked potentials (SSVEPs, Regan, 1966, 1989). The principle is very simple: presenting stimuli at a fixed rate generates a periodic EEG response at exactly the same frequency. In recent studies, individual face discrimination was assessed with this method by presenting short sequences (i.e., 60 s) of same or different faces at a specific frequency (i.e., 4 Hz = 4 faces per second) through sinusoidal contrast modulation (Rossion & Boremanse, 2011; Rossion, Alonso Prieto, Boremanse, Kuefner, & Van Belle, 2012; Prieto, Van Belle, Liu-Shuang, Norcia, & Rossion, *In press*). In these studies, a robust EEG response at the stimulation frequency (i.e., 4 Hz in the EEG frequency spectrum) was larger when different faces were shown than when the same face was repeated, even though face identity was task-irrelevant (fixation-cross color change detection). This difference was the largest over the right occipito-temporal cortex and was significantly reduced following picture-plane inversion (Rossion & Boremanse, 2011; Rossion et al., 2012) and contrast-reversal (Rossion et al., 2012). The combination of its topography and the presence of face-specific effects indicate that this difference can be taken as an objective and sensitive index of individual face discrimination. The objectivity of this approach derives from the fact that the response is measured exactly at a predefined experimental frequency. Hence, responses at other frequencies in the EEG spectrum, even at neighboring frequencies, e.g., 3.8 Hz or 4.2 Hz, can be disregarded as noise (see Rossion & Boremanse, 2011, Rossion et al., 2012 for a more in-depth discussion of the advantages of the fast periodic visual stimulation approach in high-level vision).

The aim of the current study is to extend this previous work and to provide an improved, more efficient method to measure visual discrimination by using a *fast periodic oddball* paradigm. This method measures the discrimination between base and oddball stimuli, differing on a dimension of interest (e.g., orientation, color, shape...), that are presented at two different periodicities within the same sequence. For example, base stimuli, i.e., blue dots, are shown at a constant rate (base frequency = F Hz), and oddball stimuli, i.e., red dots, are presented within the sequence of base stimuli at fixed intervals (oddball frequency = every n base stimuli or F/n Hz). Fast periodic visual stimulation is based on the assumption that a periodically presented stimulus will elicit a periodic EEG response only if this periodicity is detected by the brain. Hence, if the brain is able to differentiate base and oddball stimuli based on the manipulated dimension, i.e., blue vs. red, it would detect two periodicities (base frequency and oddball frequency) and generate two periodic responses at F Hz and F/n Hz, respectively. In contrast, if the brain does not discriminate the dimension of interest, it will produce only one

periodic response, at F Hz. Thus, the presence of a response at the oddball frequency directly reflects the discrimination of the base and oddball stimuli on the relevant dimension.

All the previous periodic face stimulation studies referred to above used a block design in which the two conditions of interest were recorded in different sequences (Rossion & Boremanse, 2011; Rossion et al., 2012; Prieto et al., *In press*). However, evaluating discrimination based on a “different–same” subtraction assumes that participants maintain the same level of attention/arousal to sequences of the exact same faces compared to those of different faces. This, of course, might not necessarily be the case and there is always a concern that noise could affect one condition more than the other. The periodic oddball approach may overcome this limitation by collapsing the “same” and “different” conditions within the same sequence. Discrimination is then indexed by the presence of a significant response at the oddball frequency, which encapsulates the “different–same” subtraction.

An additional aim of the current study is to test whether discrimination responses can be obtained for high-level stimuli and in the absence of explicit processing of the oddball stimuli. This approach based on periodic stimulation and two embedded frequency rates has been previously used to measure sensitivity to low-level visual properties in infants, such as orientation selectivity (Braddick, Wattam-Bell, & Atkinson, 1986; Braddick, Birtles, Wattam-Bell, & Atkinson, 2005) and motion direction selectivity (Braddick et al., 2005). More recently, two studies have used a similar logic in adults in the context of an oddball paradigm (orientation selectivity: Heinrich, Mell, & Bach, 2009; color: Hönegger et al., 2011). However, to the best of our knowledge, this approach has not been used to measure high-level visual processes, and in particular the discrimination of complex visual patterns such as faces. Moreover, in these latter two studies (Heinrich et al., 2009; Hönegger et al., 2011), participants were explicitly instructed to attend to the oddball stimuli.

In the present study, individual faces were sinusoidally contrast-modulated at a frequency of 5.88 Hz (base frequency F) for 60 s. This stimulation was expected to lead to a large EEG response confined to the 5.88 Hz stimulation frequency, reflecting the appearance of a face on the background (i.e., face onset; Prieto et al., *In press*). The same base face (A) was repeated throughout a sequence. Within this sequence, different oddball faces (B, C, D...) were introduced periodically, at a rate of every 5th base face, so at an oddball frequency of 1.18 Hz ($F/5 = 5.88 \text{ Hz}/5$). A sequence was therefore structured as follows: AAAABAAAACAAAAD... We hypothesized that if individual faces were visually discriminated, there would be a periodic EEG response exactly at the frequency of the oddball faces, i.e., 1.18 Hz, in brain regions coding for individual faces (i.e., the occipito-temporal cortex). Since the actual waveform of the oddball stimulation is a square-wave with a duty cycle of 20%, we expected the EEG response to also contain harmonic frequencies of 1.18 Hz (i.e., integer multiples of 1.18 Hz: $2F/5 = 2.35 \text{ Hz}$, $3F/5 = 3.53 \text{ Hz}$...). In the frequency-domain, this would correspond to a peak in the EEG amplitude spectrum at exactly 1.18 Hz and its harmonics. Critically, in order to demonstrate that these oddball responses reflect high-level face processing, we manipulated face orientation (Experiment 1: upright vs. inverted) and contrast polarity (Experiment 2: normal contrast vs. contrast-reversed). Since these manipulations lead to face-specific discrimination impairments, we predicted that they would specifically reduce the 1.18 Hz oddball response over face-related regions.

2. Experiment 1: Upright vs. inverted faces

2.1. Materials and methods

2.1.1. Participants

Twelve participants (5 males, mean age = 24 ± 4 , range = 19–37), all of whom gave written informed consent and received financial compensation for their participation, were tested in the experiment. The experimental and consenting

procedures were approved by the Biomedical Ethics Committee of the University of Louvain. One participant was excluded due to excessive blinking and the data of 11 participants were retained for analyses. They were all right-handed and reported normal/corrected-to-normal vision. None reported any history of psychiatric or neurological disorders. Participants were unaware that a face change occurred at a periodic rate of 1 out of 5 faces.

2.1.2. Stimuli

Full-front colored photographs of 25 male and 25 female faces with a neutral expression, taken under standardized conditions with respect to lighting, background, and distance from the camera were used. External features such as hair and ears were cropped out using Adobe Photoshop, and the isolated faces were put against a neutral grey background. Final images were resized to a height of 250 pixels (width = 186 ± 11 pixels). At a distance of 1 m, displayed with an 800×600 pixel resolution, they had an average size of 6.53×4 degrees of visual angle. For the inverted condition, faces were vertically flipped. Mean luminance of the faces was equalized online during stimulation and a gamma correction was applied.

2.1.3. Procedure

Fig. 1A shows a schematic illustration of the experimental design. The experiment comprised eight 65 s trials, with four trials per orientation (upright or inverted), presented in random order across participants (9 min of recording + breaks). At each orientation, there were two trials with male and two trials with female faces. Rather than numerous short trials, a small number of long duration trials were used to obtain a fine frequency resolution. This has the advantage of concentrating the responses of interest into discrete frequency bins, thus enhancing their signal-to-noise ratio (SNR) relative to the biological noise distributed randomly throughout the entire spectrum (Regan, 1989; Sutoyo & Srinivasan, 2009; Rossion et al., 2012).

A custom script running in MATLAB (based on the PsychToolbox as well as custom graphics toolboxes) was used to display the stimuli at a rate of 5.88 cycles per second ($5.88 \text{ Hz} = \text{base stimulation frequency}$) through sinusoidal contrast modulation (Rossion & Boremanse, 2011; Rossion et al., 2012). Each cycle lasted 170 ms (i.e., $1000 \text{ ms}/5.88$) and began with a uniform grey background (40 cd/m^2) from which a face appeared as its contrast increased. Full contrast was reached at 85 ms and then decreased at the same rate. To avoid confounding changes in face identity with changes with local pixel intensity changes (e.g., blue eyes vs. brown eyes), face size varied randomly between 74% and 120% in 2% steps at every 5.88 Hz stimulation cycle so that the low-level features of the faces did not overlap. A frequency of 5.88 Hz was selected as the base stimulation frequency because individual face discrimination effects are the largest at that frequency rate (Prieto et al., *In press*). The stimulation frequency was an exact integer submultiple of the 100 Hz video frame-rate ($100/17 = 5.88$).

On every trial, one face was randomly selected as the base face (A) and repeated throughout the sequence. At fixed intervals of every 5th base face, a different oddball face selected from the remaining 24 faces was presented (B, C, D...). Thus, a trial sequence contained face changes at a frequency of 5.88/5 Hz or 1.18 Hz (i.e., AAAABAAAACAAAAD...). As a result, the EEG amplitude at precisely this oddball frequency ($F/5 = 1.18 \text{ Hz}$) and its harmonics (i.e., $2F/5 = 2.35 \text{ Hz}$, $3F/5 = 3.53 \text{ Hz}$...) was used as an index of the visual system's discrimination of individual faces.

During EEG recording, participants were seated comfortably at a distance of 1 m from a CRT computer screen and were instructed to fixate on a small red cross situated in the center of the face stimuli, just below the eyes. Their task was to detect brief (200 ms) color-changes of this fixation-cross (red to blue). Color-changes randomly occurred eight times within every trial. This task was orthogonal to the manipulation of interest in the study and served the purpose of ensuring that the participant maintained a constant level of attention throughout the experiment. There were no significant differences in correct response time ($t(10) = -0.92$, $p = 0.38$) or accuracy ($t(10) = -1.3$, $p = 0.22$) in this orthogonal task between conditions. In order to avoid attention being limited to the fixation-cross, participants were also instructed to pay attention to the faces.

Fig. 1B illustrates the full time-line of a trial: following a fixation-cross displayed for 2–5 s (duration randomly jittered between trials), the sequence of faces was presented for 60 s. At the end of the trial, the stimulation gradually faded out by progressively decreasing the modulation depth from 100% maximum contrast level to 0% in 5 s. The stimulus fade-out was used to avoid abrupt eye-movements or blinks near the end of a trial. Triggers were sent via parallel port at the start of the each sequence and at the minima of each cycle (grey background, 0% contrast), and their accuracy was registered by a photodiode located in the upper left corner of the monitor. Recordings were manually initiated when participants showed an artifact-free EEG signal and each trial recording included approximately 10 s of EEG before and after the stimulus sequence.

2.1.4. EEG acquisition

EEG was acquired with a 128 Ag/AgCl electrode cap (Waveguard, ANT), that included both standard 10–20 system locations as well as additional intermediate positions. Impedance was reduced below $10 \text{ k}\Omega$ for each electrode by softly abrading the scalp with a blunt needle and injecting the electrode with saline gel. Eye-movements were monitored using four electrodes placed at the outer canthi of the eyes and above and below the right eye. An electrode linked to the ground was placed on above the nasion and all channels were referenced to AFz. The EEG recording was digitized at a 1000 Hz (128 channel high-speed amplifier, Advanced Neuro Technology, The Netherlands) 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 $\sim 270 \text{ Hz}$).

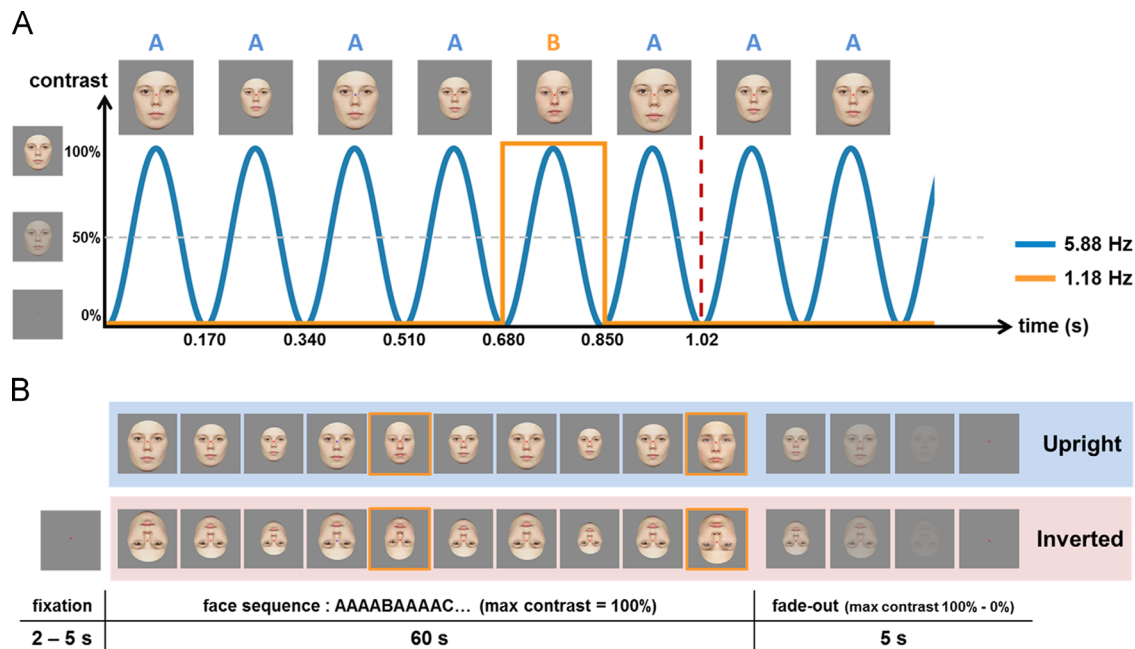


Fig. 1. Schematic illustration of the experimental paradigm. (A) Faces were presented by sinusoidal contrast modulation at a rate of 5.88 cycles per second ($= 5.88 \text{ Hz}$, so 1 cycle $\approx 170 \text{ ms}$). Base faces (A) were the same but at fixed intervals of every 5th base face ($= 5.88/5 \text{ Hz} = 1.18 \text{ Hz}$), different oddball faces (B) were presented. The identity of the base face A was randomly selected at the start of each trial. Different oddball faces, randomly selected from the remaining faces, varied every 1.18 Hz cycle. To avoid pixel-wise overlap, face size was randomly varied between 74% and 120% at every stimulation cycle. (B) Timeline of a trial: a fixation cross appeared on the screen for 2–5 s (duration randomly jittered between trials), after which faces were shown at a rate of 5.88 Hz for 60 s. At the end of the sequence, the modulation depth (i.e., maximal contrast) of the sinusoidal stimulation constantly decreased for 5 s until face stimuli completely disappeared. Participants were asked to fixate on the cross positioned between the eyes of the face stimuli and to respond to rare non-periodic fixation-cross color changes. The two conditions of Experiment 1 are displayed on the figure.

2.1.5. EEG preprocessing

All EEG processing steps were carried out using BV Analyzer 2 (Brain Products, Germany), Letswave (<http://nociions.webnode.com/letswave>; Mouraux & Iannetti, 2008), and Matlab 7.8 (The Mathworks). EEG data was digitally band-pass filtered at a high-pass cut-off of 0.1 Hz and a low-pass cut-off of 100 Hz using a Butterworth filter with a slope of 24 dB/octet. Filtered data was then segmented 2 s before and after the sequence, resulting in 69 s segments (−2–67 s). Data files were then downsampled to 250 Hz to reduce the file size and data processing time. The two mastoid electrodes (M1 and M2) were deleted from the EEG data because of excessive noise in these channels. Next, noisy or artifact-ridden channels were re-estimated using linear interpolation (no more than 5% of channels were pooled for a given trial) and a common average reference computation was applied to all channels.

2.1.6. Frequency domain analysis

Preprocessed data segments were cropped down to an integer number of 1.18 Hz cycles beginning 2 s after onset of the trial until approximately 59.83 s, just before the stimulus fade-out (68 cycles, 14458 time bins in total ≈ 58 s). The first 2 s of each trial were excluded to avoid any contamination by the initial transient responses. Trials were averaged in the time-domain, separately for each orientation condition (upright or inverted, four trials per orientation) and each individual participant's data. This averaging was performed to increase the SNR by reducing EEG activity non-phase-locked to the stimulus. A fast Fourier transform (FFT) was then applied to these averaged segments and amplitude spectra were extracted for all channels (square root of the sum of squares of the real and imaginary parts divided by the number of data points, see [Supplementary figure and table for amplitude data](#)). Thanks to the long time-window (57.83 s), frequency analysis yielded spectra with a high frequency resolution of 0.0173 Hz (1/57.83), thus improving SNR and allowing unambiguous identification of the response at the frequencies of interest (i.e., 5.88 Hz, 1.18 Hz, and their harmonics). For analyses focusing on responses related to individual face discrimination, we excluded the 5th harmonic of 1.18 Hz (5.88 Hz) from the analysis because the general

response to face onset/offset and the individualization response are confounded at this frequency.

SNR was computed to take into account the variations of noise across the EEG spectrum. SNR was calculated as the ratio of the amplitude at each frequency to the average of the 20 surrounding frequency bins (10 on each side, excluding the immediately adjacent bin) (e.g., as applied in [Srinivasan, Russell, Edelman, & Tononi, 1999](#); [Rossion et al., 2012](#)). Z-scores were also calculated in the same way (difference between amplitude at the frequency of interest and mean amplitude of 20 surrounding frequency bins divided by the standard deviation of the 20 surrounding bins). Threshold of significance was placed at a Z-score of 1.96 ($p < 0.05$).

For the group analysis, individual SNR spectra were averaged within each orientation condition. Group Z-scores were calculated by averaging individual amplitude spectra, then computing Z-scores on the resulting grand-averaged amplitude spectrum in the same way as described above.

2.1.7. ROI analysis

Channels were divided into 13 regions-of-interest (ROI) in order to explore the scalp distribution of EEG responses ([Fig. 3C](#)). SNR values of channels within each ROI were averaged for each participant and each condition, and grand-averaged for data display. To assess whether there was a significant response at the fundamental stimulation frequency or at its harmonics, Z-scores were calculated on the grand-averaged amplitude values for each ROI.

2.1.8. Statistical comparisons of conditions

ROI analysis and Z-scores were used to establish the significance (i.e., presence) of a response at a given stimulation frequency and in a given ROI so that these responses could be considered in a comparison of conditions. To determine the number of harmonic frequencies to take into account, Z-scores were computed over the average of all 126 channels in each condition. Harmonics were analyzed until they were no longer significant in either condition. Analyses of individual

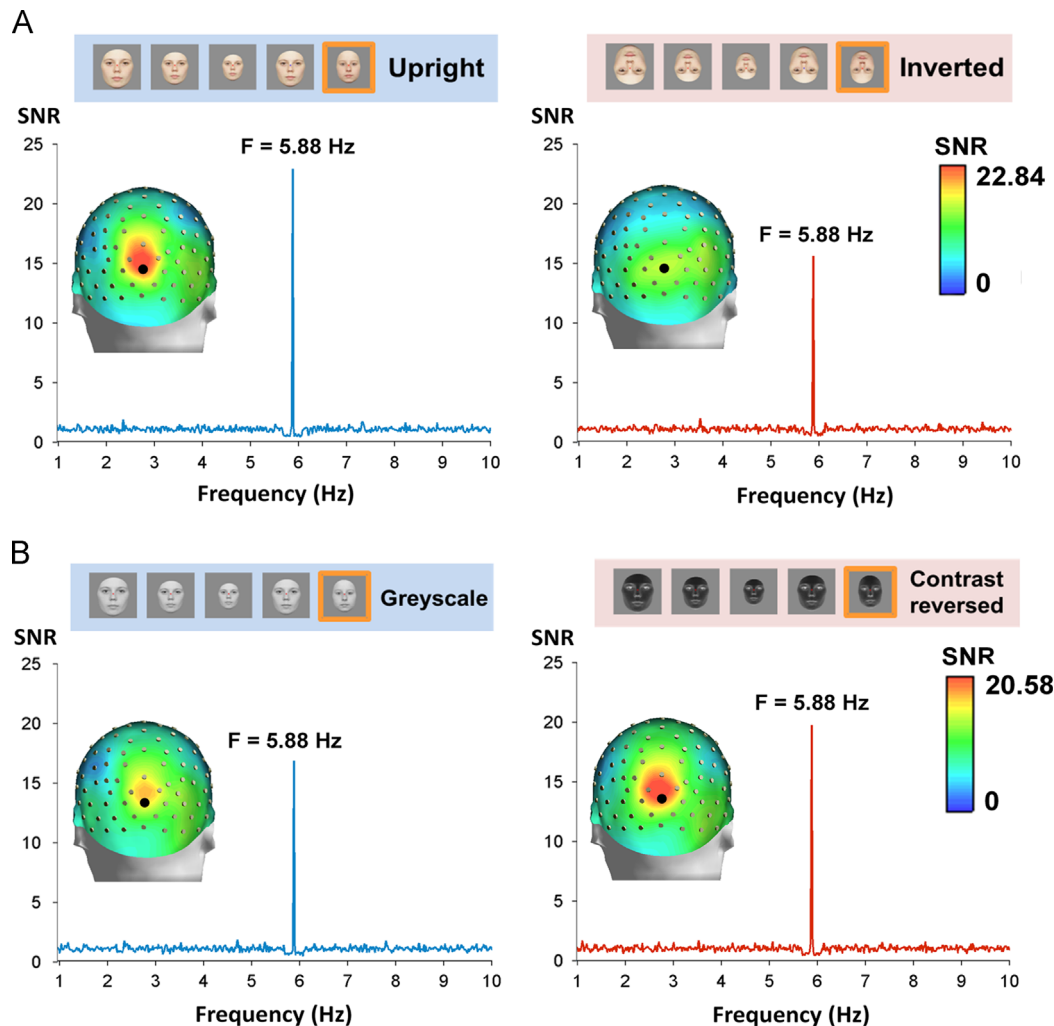


Fig. 2. Grand-averaged SNR at the base stimulation frequency of 5.88 Hz. The 3D topographies are shown on a common color scale (far right) for each pair of conditions in both experiments. Activity at this frequency was mainly concentrated around the medial occipital channels. The spectra show the SNR values for medial occipital channel Oz (indicated by a black dot on 3D topographies). (A). Experiment 1: upright (left) vs. inverted faces (right). (B) Experiment 2: greyscale (left) vs. contrast-reversed faces (right).

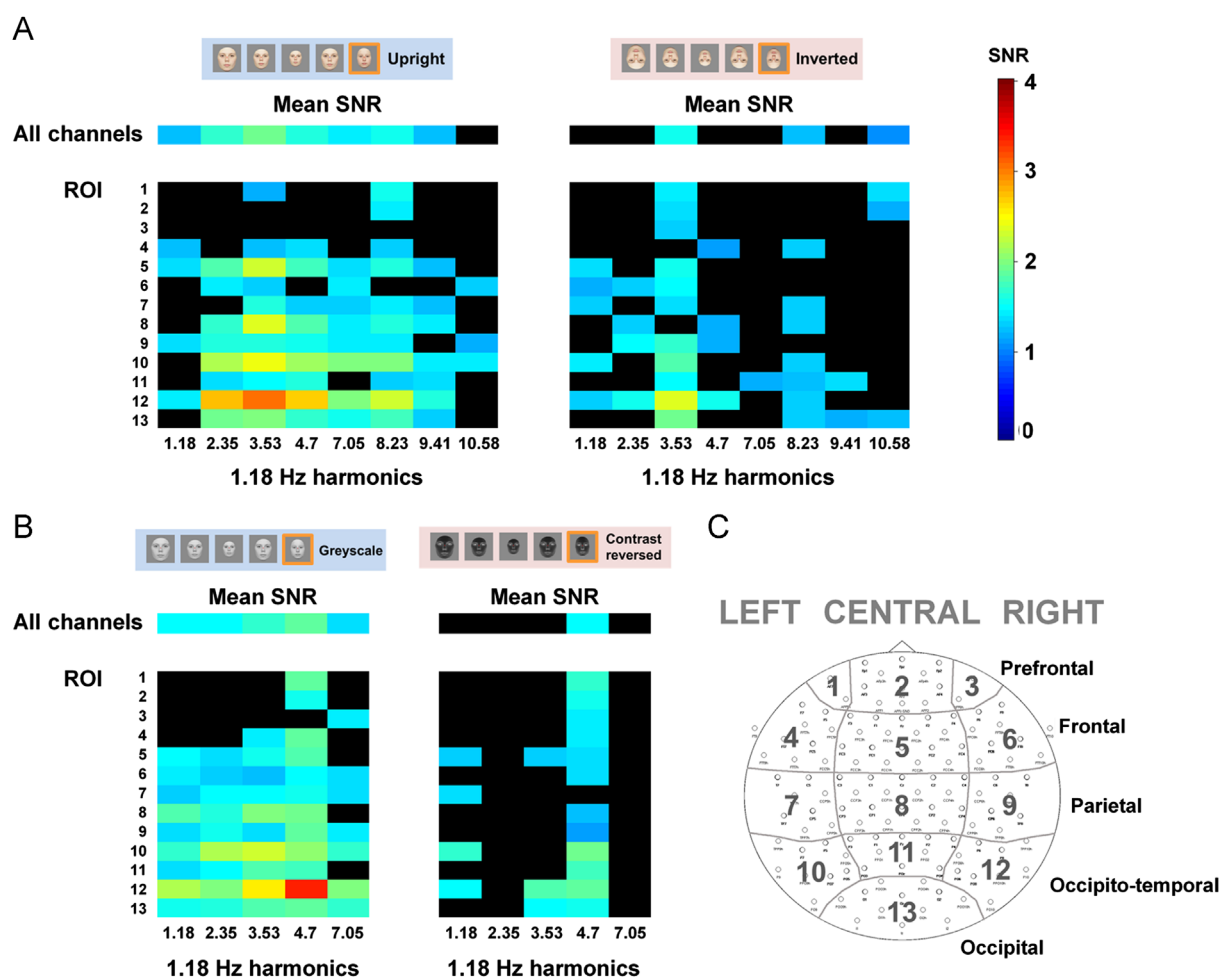


Fig. 3. Responses at the oddball face discrimination frequency ($F/5=1.18$ Hz) and its harmonic frequencies ($2F/5=2.35$ Hz, $3F/5=3.53$ Hz...) presented for Experiment 1 (A) and Experiment 2 (B). The top rows show the mean SNR at each frequency averaged across all 126 channels. The bottom matrices show the mean SNR averaged by frequency and by regions-of-interest (ROI; 13 in total). The ROIs are shown schematically in (C). The 5th harmonic of the oddball frequency ($F=5.88$ Hz) was not taken into account since it was confounded with the base stimulation frequency. Matrix cells are color-coded according to their SNR value (see far right for color scale). Black cells indicate regions and frequencies at which no significant responses were found, as assessed by Z-scores with a threshold of $Z\text{-score} > 1.96$ ($p < 0.05$).

participant data followed the same thresholds as those for the group data. For responses at the face discrimination frequency, SNRs of significant harmonics were averaged together since they were strictly related to the same phenomenon (e.g., Appelbaum, Wade, Vildavski, Pettet, & Norcia, 2006; Heinrich et al., 2009). Statistical comparison between conditions was performed with pairwise t -tests. When testing for differences at individual electrodes, multiple comparison error was controlled by only taking into account channel clusters containing a minimum of three channels with significant effects at a threshold of $p < 0.01$.

2.1.9. Time-domain analysis

EEG data was also analyzed in the time-domain using time segments from 2.55 s after stimulus onset until 53.57 s (≈ 300 cycles of 5.88 Hz). The first 15 cycles (2250 ms) were excluded so that potential variations due to the build-up of steady-state response to oddball face change would not contaminate data. The resulting 51 s segments were divided into 6 epochs of 50 stimulation cycles, so 8.5 s in length ($50 \times 170 \text{ ms} = 8.5 \text{ s}$), which corresponded to 10 repetitions of an AAAAB sequence (5 oddball face changes). Epochs were then averaged together and low-pass filtered at 10 Hz (FFT filter, width=2 Hz). This analysis was carried out on the individual participants and then averaged to display group data.

2.2. Results

2.2.1. Upright faces: Base stimulation frequency (5.88 Hz)

Grand-averaged SNR spectra showed clear responses at the 5.88 Hz stimulation frequency (mean $\text{SNR} \pm \text{SEM} = 7.23 \pm 0.36$), thus demonstrating successful synchronization to the visual stimulation. The statistical reliability of these responses was high (Z-score range across channels=5.72–101.15). In addition to the fundamental response at

5.88 Hz, there were significant responses up to the 6th harmonic ($6F=35.27$ Hz), with gradually decreasing SNR values (Table 1). Overall, the response at 5.88 Hz had a medial occipital topography, peaking on electrode Oz (SNR=22.84; Fig. 2A left). This scalp topography is typical of SSVEP responses to low-level visual stimuli, often obtained with higher frequency rates (e.g., Srinivasan et al., 1999). A similar topography was also previously observed when repeating a same face at this frequency rate (Rossion & Boremanse, 2011; Rossion et al., 2012; Prieto et al., In press). Since the main focus of the current experiment concerns responses at the oddball face discrimination frequency, the 5.88 Hz response will not be further analyzed.

2.2.2. Upright faces: Oddball face discrimination frequency (1.18 Hz)

2.2.2.1. Group results. Fig. 3A (left) displays the SNR of the responses at 1.18 Hz and its harmonic frequencies according to the color-scale on the right. Non-significant responses (below Z-score threshold of 1.96) are blacked out. Pooling across all channels, responses were significant from 1.18 Hz up to its 8th harmonic (9.41 Hz; Fig. 3A, top left). In terms of topographical distribution, the right occipito-temporal (rOT) ROI displayed the highest SNR values. Given this observation but also the importance of this region for individual face perception (e.g., Jacques & Rossion, 2006; Jacques, Arriape, & Rossion, 2007) the remaining analyses focused on this ROI.

Table 1
Grand-averaged SNR and Z-scores at base frequency 5.88 Hz (averaged across all channels).

(A) Experiment 1				
Frequency (Hz)	Upright		Inverted	
	Mean SNR	Z-score	Mean SNR	Z-score
1F=5.88	7.23	61.66	6.94	75.56
2F=11.76	5.82	50.43	4.96	43.26
3F=17.64	2.5	24.18	2.22	19.33
4F=23.52	1.83	13	2.04	14.82
5F=29.4	1.34	4.45	1.4	6.67
6F=35.27	1.43	6.08	1.26	5.43
(B) Experiment 2				
Frequency (Hz)	Greyscale		Contrast reversed	
	SNR	Z-score	SNR	Z-score
1F=5.88	6.68	61.27	7.82	54.64
2F=11.76	2.93	15.93	6.11	36.66
3F=17.64	2.63	23.32	3.89	42.87
4F=23.52	1.63	9.86	2.73	25.94
5F=29.4	1.23	3.72	2.22	29.97
6F=35.27	1.40	10.25	2.93	35.04
7F=41.15	1.12	2.05	2.18	20.77

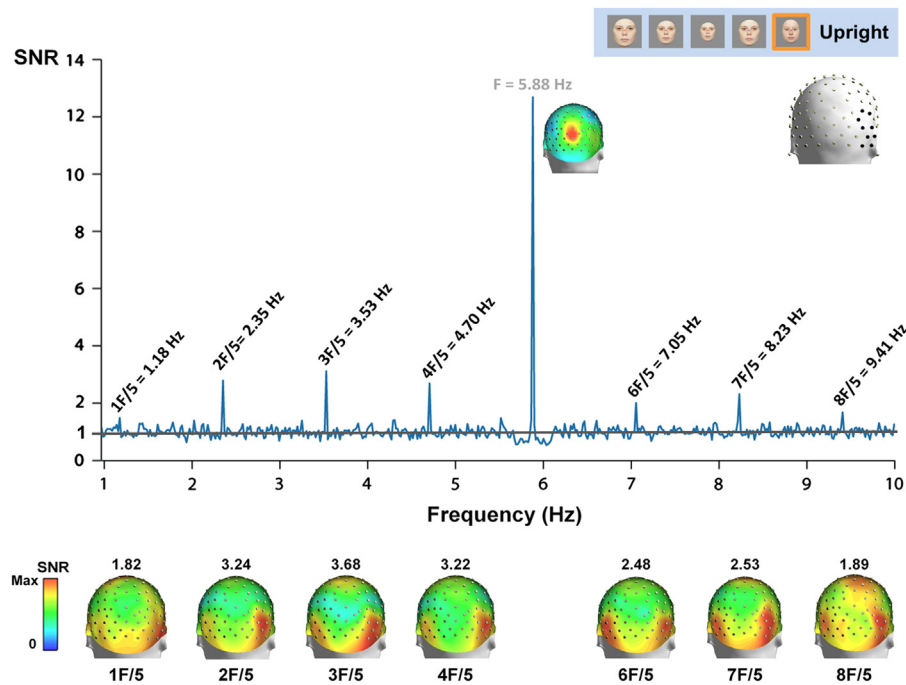


Fig. 4. SNR spectrum of the right occipito-temporal ROI for upright faces in Experiment 1. The channels composing this ROI are indicated with black dots on the blank 3D head in the upper right. On the SNR spectrum, only significant oddball responses are labeled (Z-score > 1.96). For upright faces, oddball face discrimination responses were clearly defined and significant at the fundamental frequency (1.18 Hz) and harmonics until the 8th harmonic (9.41 Hz). Note that while the 1.18 Hz response appears small, it has a SNR of 1.49, corresponding to a 49% response increase. Below the spectrum, 3D topography of each harmonic response is shown with its individual color-scale (the scales' maxima, corresponding to the maximal SNR value, are shown above each topography). All topographical maps showed higher oddball responses over the occipito-temporal regions, with a clear right hemisphere lateralization.

The frequency spectra of the rOT ROI can be seen in Fig. 4. Responses at harmonic frequencies of the 1.18 Hz oddball frequency are clearly visible. Below the spectrum for the rOT ROI, scalp topographies of each harmonic of 1.18 Hz show a very similar topographical distribution. Unlike the 5.88 Hz response (Fig. 2A), the 1.18 Hz harmonics peaked on bilateral occipito-temporal regions, with a strong right hemisphere lateralization (Fig. 4). There was also a fronto-central response for most harmonic frequencies (central parietal and central frontal ROIs, Fig. 3A). SNR values varied

substantially between the different harmonics, with the largest SNR occurring at the 3rd harmonic (3.53 Hz) and the smallest at the fundamental or first harmonic (1.18 Hz). Nevertheless, even this “small” response was highly significant (Z-score=3.32) and clearly above noise level, with a SNR of 1.49 corresponding to a response increase of nearly 50% compared to neighboring frequencies.

To test the robustness of the response, we performed a complementary analysis of group data with only a single 60 s trial. Despite this limited data set, significant responses at face

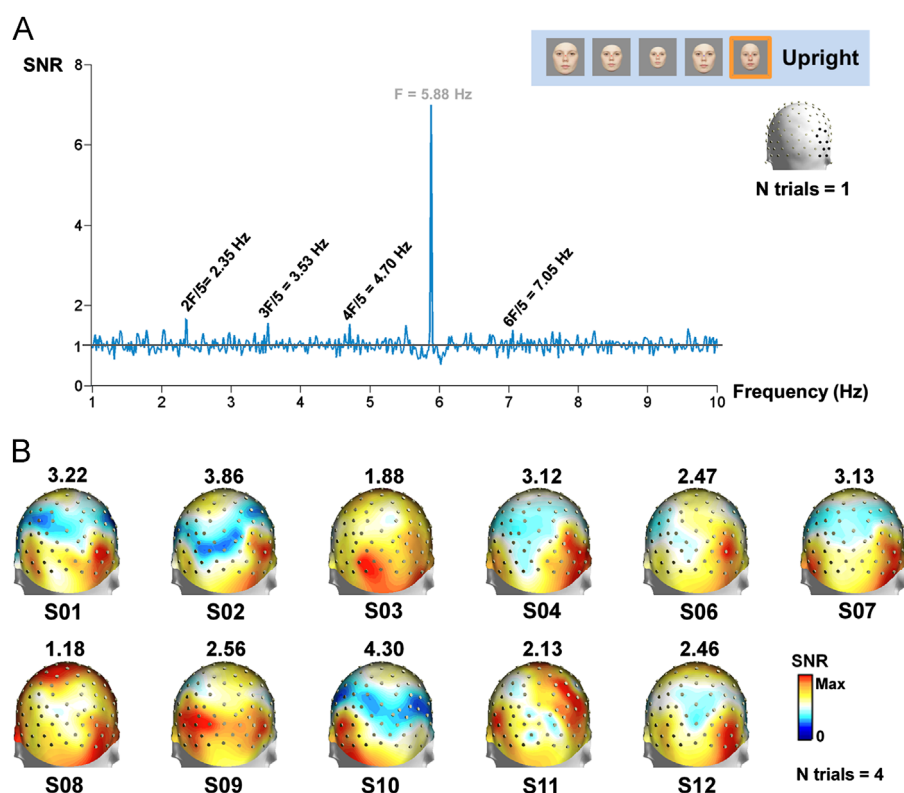


Fig. 5. (A) Grand-average SNR spectrum for a single trial (60 s of recording) in the upright condition for the right occipito-temporal ROI (channels shown on the blank 3D topography on the right) in Experiment 1. Only significant responses are labeled (Z -score > 1.96). (B) 3D topographies of oddball responses in individual participants (average of 4 trials). SNR values of harmonic frequencies that were significant on the group-level were averaged ($1F/5 = 1.18$ Hz until $8F/5 = 9.41$ Hz, excluding 5.88 Hz). The color-scale represents response magnitude according to individual participants' peak SNR value, which is shown above each topography.

discrimination were still present (Fig. 5A), albeit fewer in number than for the average of four trials.

2.2.2.2. Sensitivity at the individual level for upright faces. Despite substantial inter-individual variation in SNR, there were significant oddball face discrimination responses in the rOT ROI for every participant (Z -score range = 2–12.16). The mean SNR of individually significant harmonics ranged from 1.86 to 4.23. The highest SNR values were also observed in this region in 8 out of 11 participants (Fig. 5B). For the three remaining participants, two (S09 & S10) showed significant responses in the left occipito-temporal ROI and one (S08) showed a significant response in the central ROI.

2.2.2.3. Time-domain analysis. At the right occipito-temporal site P8, systematic negative deflections following the presentation of the oddball faces were observed on bandpass-filtered EEG data. These negative deflections appeared at fixed intervals of exactly five cycles (Fig. 6A & B). Furthermore, individual participant data show only modest inter-subject variation in terms of pattern and response latency (Fig. 6C), with the exception of S11, whose response was out of phase, and S08, whose response was weak and out of phase. These well-defined temporal markers complement the frequency-domain analysis and support the view that the response in this region directly reflects face individualization. Interestingly, the EEG waveform over the medial occipital cortex (Oz) did not reveal any such enhanced response following the presentation of oddball faces (Fig. 6D).

Although the face discrimination response was the highest at occipito-temporal sites, strong responses were also observed at centro-frontal regions (Fig. 3A). At the central electrode Cz, positive responses at approximately the same intervals as at right occipito-temporal channels were observed, i.e., every 5th cycle (Fig. 6A). Similar observations apply to Fz (not shown). Although the overall response

(i.e., 5.88 Hz cycles) was much weaker, responses to oddball faces seemed nevertheless well synchronized with the responses on P8. The presence of systematic positive deflections on Cz and Fz (i.e., polarity reversal with respect to the P8 negative deflections) implies that they may have a common functional origin with the posterior face discrimination response.

2.2.3. Upright faces: Summary of results

In summary, introducing different oddball faces at a fixed rate (every 850 ms or 1.18 Hz) within a sequence of identical base faces (shown every 170 ms or 5.88 Hz) elicits large periodic responses at the exact frequency of face change and at its harmonics, especially in the right occipito-temporal region. These responses were found in every individual participant, with substantial variability in response strength, but remarkable consistency in terms of scalp topography. Time-domain analyses revealed systematic negative deflections over the right occipito-temporal area at the same rate at which different oddball faces were presented (every 5th face). These observations demonstrate that a fast periodic oddball paradigm can be successfully used to objectively measure individual face discrimination, and do so in an extremely efficient manner: four 60 s trials were sufficient to obtain reliable responses in every participant.

2.2.4. Inverted faces: Base stimulation frequency (5.88 Hz)

As for upright faces, there were highly significant responses at 5.88 Hz for inverted faces (Z -score range across channels = 9.94–95.07; mean SNR \pm SEM = 6.94 ± 0.27 ; see Table 1 & Fig. 2A, right). Harmonic frequencies were also present until the 6th harmonic (35.27 Hz). The topographical distribution of responses was also centered on Oz (SNR = 15.51).

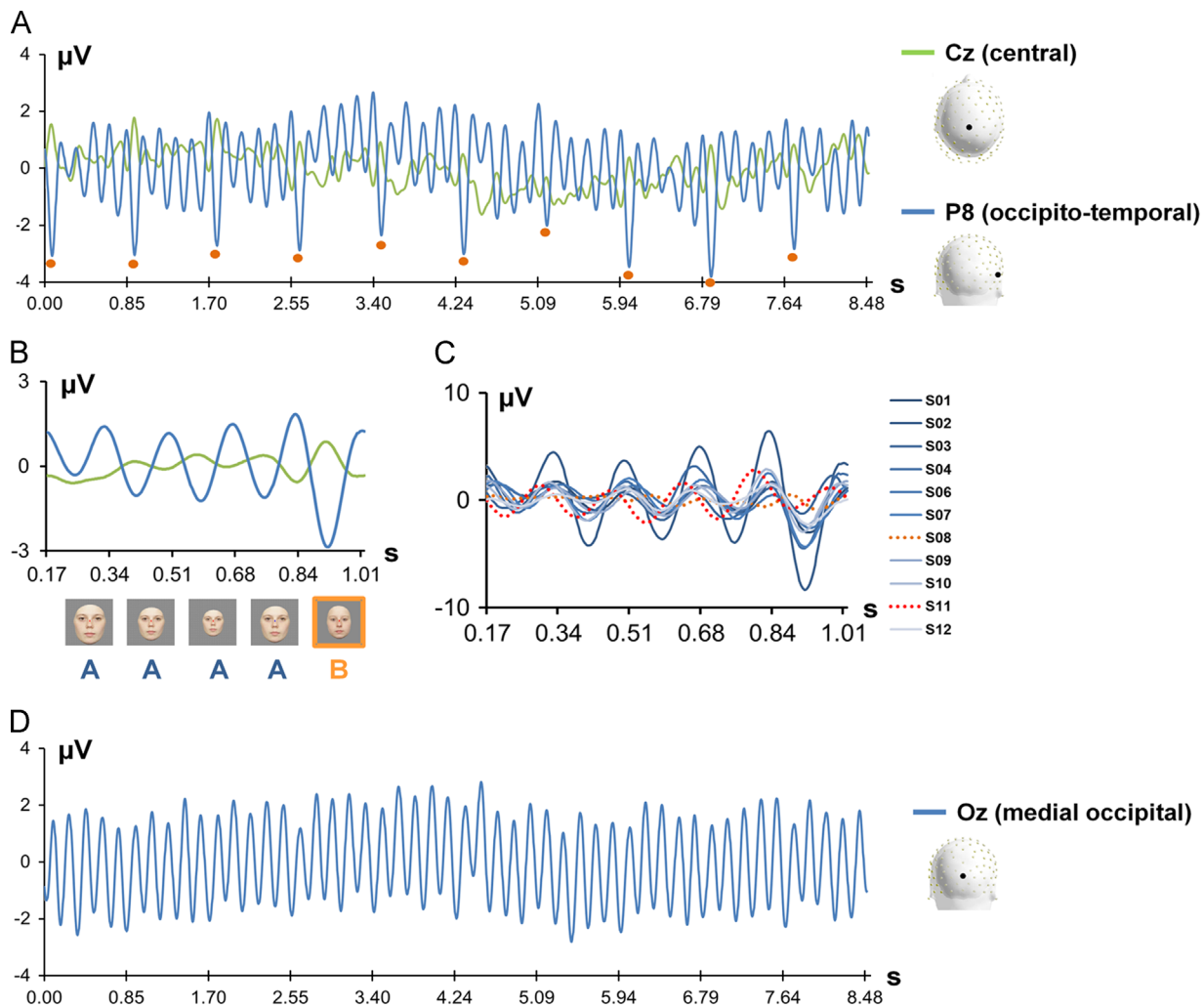


Fig. 6. Responses to upright faces represented in the time-domain in Experiment 1. Each graph represents the average response to a segment containing 10 oddball face changes ($10 \times \text{AAAAB}$ sequence). The positions of electrodes represented by the graphs are shown on the right. (A) Grand-average EEG waveform for channels P8 and Cz. Clear periodic responses corresponding to each face presentation at the 5.88 Hz stimulation rate can be seen. Orange dots indicate negative deflections occurring at the exact same intervals as the oddball face changes (i.e., every 5th cycle). Although the overall response is less consistent, oddball face responses can also be observed on Cz, with a phase reversal. (B) Grand-average EEG waveform averaged over one oddball sequence ($1 \times \text{AAAAB}$) on channels P8 (blue) and Cz (green). (C) Individual responses during one oddball sequence on channel P8. Despite some inter-individual variability, responses are well in phase and a negative deflection following oddball face change is present in the majority of subjects (except for out-of-phase responses from S11 and weak and out-of-phase responses from S08, shown in red and orange dotted lines, respectively). (D) Grand-average EEG waveform on Oz. No oddball face discrimination peaks can be distinguished, thus reinforcing the hypothesis that signal at the oddball frequency cannot be attributed to low-level visual processing. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2.5. Inverted faces: Face discrimination frequency (1.18 Hz)

Face inversion strongly impairs face discrimination while maintaining the same low-level visual properties as upright faces (e.g., Yin, 1969). Since we hypothesized that the oddball response reflected high-level face identity processing, we expected that it would be much smaller in this condition.

2.2.5.1. Group results. On grand-averaged data, the responses related to the discrimination of inverted individual faces were much weaker and significant only at a few harmonics (Fig. 3A, left; Fig. 7). Notably, scalp topography of the significant responses was similar to that of the upright condition (Fig. 7).

2.2.5.2. Sensitivity at the individual level for inverted faces. At the individual level, fewer harmonics were significant in the right occipito-temporal (rOT) ROI (Z-score range = 2.11–7.0), and one participant did not show any face discrimination response at all. Mean SNR of individually significant harmonics ranged from 1.84 to 3.62. Furthermore, SNR values peaked in this area

in only 6 out of 11 participants. The largest face discrimination responses were thus clustered in the following ROIs for the remaining participants: left occipito-temporal (S01 & S10), medial occipital (S03), medial occipito-temporal (S08), and left prefrontal (S09).

2.2.6. Upright vs. inverted faces

2.2.6.1. Base stimulation frequency (5.88 Hz). Averaging across all channels, SNR did not differ significantly between conditions ($t(10) = 0.31, p = 0.76$, two-tailed). Locally, upright faces elicited a larger 5.88 Hz response compared to inverted faces only on the medial occipital region (Fig. 2A). Channel-wise comparison revealed significant differences only at a cluster of 5 contiguous channels in this area (P1, Pz, PPO1, PPO2, POO3h, Oz; p -value range = 0.01–0.005)¹.

¹ Only one right temporal electrode also exhibited significant differences (TPP8h, $p < 0.008$), but it was not taken into account given our predefined selection criteria (minimum of 3 contiguous channels).

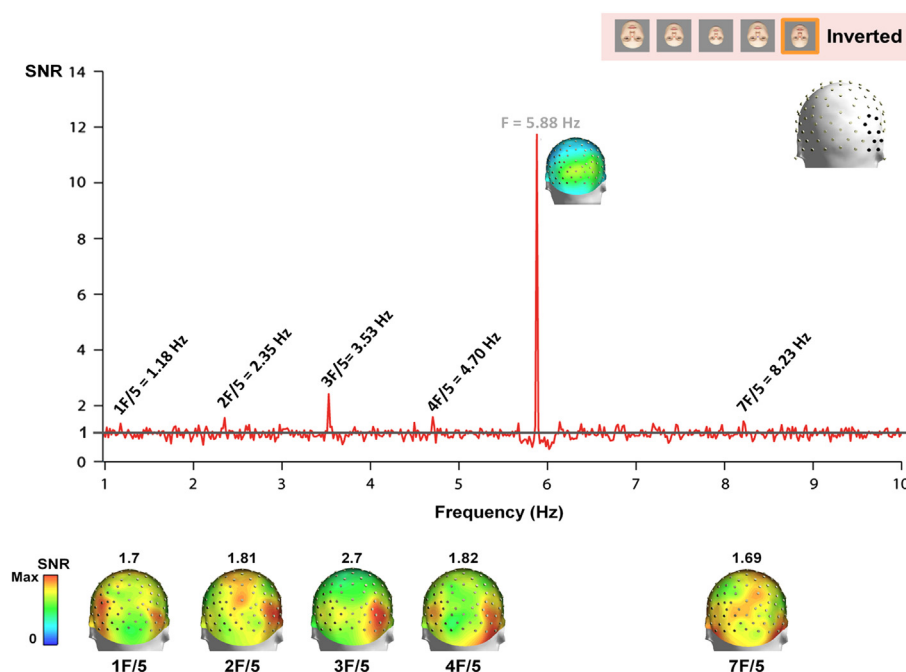


Fig. 7. SNR spectrum of the right occipito-temporal ROI for inverted faces in Experiment 1. The channels composing this ROI are indicated with black dots on the blank 3D head in the upper right. On the SNR spectrum, only significant responses (Z -score > 1.96) are labeled. Below the spectrum, 3D topography of each harmonic is shown at its individual color scale (the scales' maxima correspond to the maximal SNR value for each topography).

2.2.6.2. Face discrimination frequency (1.18 Hz). Only harmonics that were commonly significant in both conditions in the rOT ROI for the group analysis were considered and averaged for statistical comparison (i.e., 1.18 Hz, 2.35 Hz, 3.53 Hz, 4.70 Hz, and 8.23 Hz). Responses related to oddball face discrimination were significantly larger for upright compared to inverted faces ($t(10)=4.8$, $p < 0.0003$; Fig. 8A & C). This difference was specific to the face discrimination frequency: the responses at the 5.88 Hz base stimulation frequency did not differ between conditions in this ROI ($t(10)=0.41$, $p=0.34$; Fig. 8C). A larger response in the upright condition was also present for 11 out of 12 participants. Notably, the only participant (S08) for whom no advantage was found for upright as compared to inverted faces had very small discrimination responses in the rOT for both conditions (Table 2).

To summarize, responses reflecting the individual face discrimination frequency over the right occipito-temporal cortex were much larger and more consistent across harmonics and participants for upright relative to inverted faces. Interestingly, this difference was found despite that there were no differences between upright and inverted faces at the base stimulation frequency (5.88 Hz), neither overall or specifically at the right occipito-temporal region. It is noteworthy that the 1.18 Hz oddball response and the 5.88 Hz base response were not correlated. Significant 1.18 Hz responses in the rOT ROI for upright faces did not show significant correlations with the 5.88 response either within the rOT (upright: $r=0.47$, $p=0.14$; inverted: $r=0.45$, $p=0.17$) or in the medial occipital region (upright: $r=0.10$, $p=0.76$; inverted: $r=0.49$, $p=0.13$).

3. Experiment 2: Grayscale vs. contrast-reversed faces

3.1. Purpose

Experiment 2 aimed at strengthening and generalizing the observations of Experiment 1 by using grayscale face pictures and their contrast-reversed counterparts. On the one hand, responses to grayscale faces rely on more impoverished facial

identity information (i.e., absence of color, which is information diagnostic of facial identity, e.g., Edwards, Xiao, Keyser, Földiák, & Perrett, 2003; Yip & Sinha, 2002), allowing us to test the robustness of the signal at the oddball face discrimination frequency. On the other hand, one cannot exclude that differences obtained in Experiment 1 between upright and inverted faces were influenced by the fact that different amounts of visual information were available in the upper and lower visual fields in these conditions. Indeed, since the fixation cross was maintained at the same position in both conditions (on the bridge of the nose), a larger portion of the face stimuli was presented in the lower visual field for upright than inverted faces. The topography of the base stimulation response hints at such a visual field effect: higher SNR was found for upright faces in the upper half as compared to the lower half of the medial occipital channels (Fig. 2A). Although unlikely, we cannot entirely reject the possibility that these low-level disparities could have influenced differences between conditions at the oddball face discrimination frequency. In this context, contrast-reversal, which is known to disrupt face identity discrimination (e.g., Bruce & Langton, 1994; Itier & Taylor, 2002; Russell et al., 2006), can serve as an important additional control. Contrary to orientation inversion, the fixation-cross remains at the same location for grayscale faces and contrast-reversed faces so that the spatial distribution of visual information is identical between conditions. Despite this, we hypothesized that the EEG responses related to individual face discrimination (1.18 Hz and harmonics) would be severely reduced with contrast inverted stimuli, while the responses to the basic face stimulation (5.88 Hz) would remain constant.

3.2. Methods

3.2.1. Participants

Ten participants (one male, mean age = 23 ± 3 , range = 20–29), all of whom gave written informed consent and received financial compensation for their participation in the experiment, were tested. Two of these participants took part in Experiment 1. Data from one participant was excluded due to an excessive number of artifacts, thus, nine participants were retained for analyses. All were right-

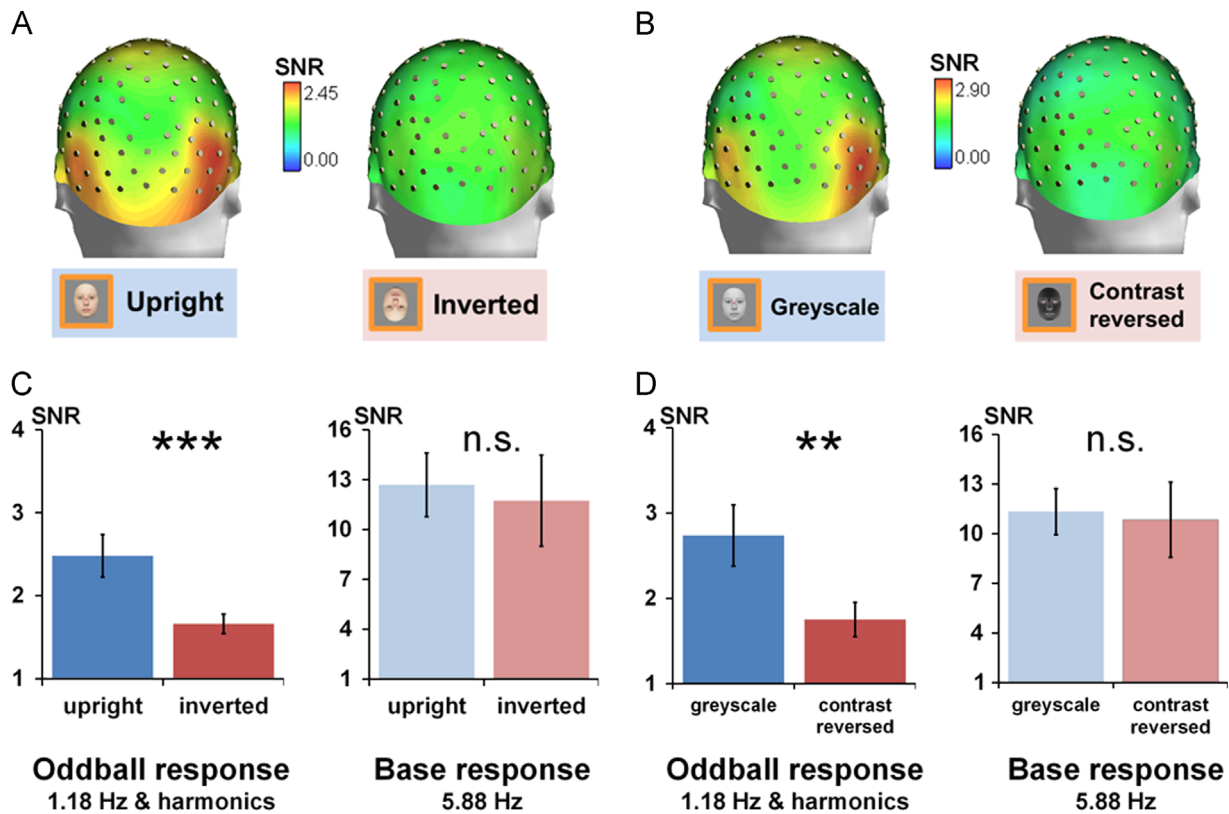


Fig. 8. Top row (A and B): 3D topographies of SNR values averaged across the range of significant oddball responses for (A). Experiment 1 (1F/5 = 1.18 Hz until 9F/5 = 10.58 Hz) and (B). Experiment 2 (1F/5 = 1.18 Hz until 6F/5 = 7.05 Hz). Activity related to face individualization was the largest over the right occipito-temporal region. Bottom row ((C) and (D)): Histogram of SNR values in the right occipito-temporal ROI at the base stimulation frequency (5.88 Hz) and common significant oddball responses across conditions: (C) Experiment 1: mean SNR of 1F/5, 2F/5, 3F/5, 4F/5 and 7F/5; (D) Experiment 2: mean SNR of 1F/5 until 6F/5. Error bars represent standard error of mean. Although the SNR was higher at 5.88 Hz, there was no difference between conditions, in contrast to the SNR at oddball frequencies (* $p < 0.01$; *** $p < 0.001$).

handed and reported normal/corrected-to-normal vision. None reported any history of psychiatric or neurological disorders.

3.2.2. Stimuli & procedure

Stimuli consisted of the same set of photographs of 25 male and 25 female faces as Experiment 1, but they were rendered into greyscale and contrast-reversed in Adobe Photoshop. The experimental design was the same as in Experiment 1, with the exception that the conditions were greyscale vs. contrast-reversed faces instead of upright vs. inverted faces; trial randomization and testing procedure were the same. Although accuracy at the fixation-cross colour-change task was slightly higher in the greyscale than the contrast-reversed condition (96% vs. 90%, $t(8) = 3.02$, $p < 0.02$) participants were also slightly slower with greyscale faces (475 ms vs. 461 ms; $t(8) = -0.94$, $p = 0.37$). Inverse efficiency (RT/accuracy rate, Townsend & Ashby, 1978) scores did not differ between conditions ($t(8) = -1.74$, $p = 0.12$) indicating a small speed-accuracy trade-off.

3.2.3. EEG acquisition & analysis

EEG acquisition parameters and data analyses were identical to Experiment 1.

3.3. Results

3.3.1. Base stimulation frequency (5.88 Hz)

Similarly to Experiment 1, robust responses were found at 5.88 Hz for both greyscale and contrast-reversed faces (mean SNR \pm SE: greyscale = 6.68 ± 2.12 ; contrast-reversed = 7.81 ± 4.11). Significant responses were also found at harmonic frequencies (Table 1). Maximal responses in both conditions were found on medial occipital channels (greyscale: Oz = 16.74; contrast-reversed: POO3h = 20.58; Fig. 2B). Although SNR values at this frequency were higher for contrast-reversed, compared to greyscale, faces in this region, there were no significant differences between conditions, neither overall ($t(8) = -1.28$, $p = 0.24$, two-tailed) nor between individual channels.

3.3.2. Face discrimination response: Greyscale faces

3.3.2.1. Group results. For greyscale faces, significant responses at the oddball frequency and its harmonics were clearly observed. However, compared to color faces (Experiment 1), there were fewer significant harmonics overall, with no significant response beyond the 6th harmonic (7.05 Hz; Fig. 3B left, top row). Once again, the highest significant SNR values were located in the right occipito-temporal (rOT) ROI (Fig. 3B left). We therefore concentrated on this area, similarly to the analysis of Experiment 1. Responses to oddball face changes were robust in this region (Fig. 9A). The SNR topography had a similar distribution across all significant harmonics (see 3D topographies below the SNR spectrum in Fig. 9A) and the right lateralization of responses was also present in this second experiment.

3.3.2.2. Sensitivity at the individual level for greyscale faces. Individual variations were also evident in Experiment 2. Nevertheless, responses related to face discrimination remained significant in all of the nine participants in the rOT ROI (Z-score range = 2.05–11.63). The mean SNR of significant harmonics for each participant varied from 1.37 to 2.36. Maximal SNR values were found in this ROI for five out of nine participants. Out of the remaining participants, two had the largest responses in the left occipito-temporal region (S04 & S08), and one each in the medial occipital (S03) and central parietal regions (S02), respectively.

3.3.3. Face discrimination response: Contrast-reversed faces

3.3.3.1. Group results. Contrast-reversal led to a substantial decrease in the overall number of significant responses and their

Table 2

Mean SNR of the response at the oddball frequency harmonics in the right occipito-temporal region-of-interest.

(A). Experiment 1		
Participant	Upright	Inverted
	Mean SNR \pm SEM	Mean SNR \pm SEM
S01	2.98 \pm 0.50	1.69 \pm 0.35
S02	3.59 \pm 0.53	2.05 \pm 0.45
S03	1.49 \pm 0.21	0.97 \pm 0.19
S04	3.10 \pm 0.38	2.22 \pm 0.36
S06	2.69 \pm 0.25	1.52 \pm 0.25
S07	3.42 \pm 0.46	2.08 \pm 0.31
S08 ^a	0.85 \pm 0.16	1.08 \pm 0.20
S09	2.18 \pm 0.30	1.59 \pm 0.41
S10	2.20 \pm 0.39	1.56 \pm 0.25
S11	1.82 \pm 0.35	1.79 \pm 0.28
S12	2.95 \pm 0.41	1.72 \pm 0.15
Group	2.48 \pm 0.36	1.66 \pm 0.17

Note. SNR averaged over 1F/5 (1.18 Hz), 2F/5 (2.35 Hz), 3F/5 (3.53 Hz), 4F/5 (4.70 Hz) and 7F/5 (8.23 Hz) oddball frequency harmonics.

B. Experiment 2		
Participants	Greyscale	Contrast reversed
	Mean SNR \pm SEM	Mean SNR \pm SEM
S02	1.93 \pm 0.43	1.54 \pm 0.32
S03	1.18 \pm 0.29	0.98 \pm 0.13
S04	3.00 \pm 0.53	1.64 \pm 0.32
S05	2.21 \pm 0.34	1.68 \pm 0.21
S06	3.54 \pm 0.44	2.83 \pm 0.42
S07	3.65 \pm 0.51	1.36 \pm 0.15
S08	4.52 \pm 0.49	2.67 \pm 0.38
S09	2.94 \pm 0.35	1.58 \pm 0.25
S10	1.67 \pm 0.20	1.49 \pm 0.29
Group	2.74 \pm 0.36	1.75 \pm 0.20

Note. SNR averaged over 1F/5 (1.18 Hz), 3F/5 (3.53 Hz), and 4F/5 (4.70 Hz) oddball frequency harmonics.

^a This participant did not show a larger response to upright than to inverted faces, however, the SNR was close to 1 in both conditions.

magnitude (Fig. 3B right). The same observations regarding the predominance of the response at the rOT ROI apply in this condition. Topography-wise, individual harmonic responses were concentrated around the lateral occipito-temporal regions, although there was no clear lateralization (Fig. 9B, bottom).

3.3.3.2. Sensitivity at the individual level for contrast-reversed faces. As in the inverted condition in Experiment 1, significant oddball face discrimination responses were present in fewer participants (7 out of 9) and at fewer harmonics in the rOT ROI (Z -score range=2.17–7.95). The mean SNR of individually significant harmonics ranged from 1.15 to 2.08. Only two out of nine participants had maximal SNR in the rOT ROI, while for the others it was found over the left occipito-temporal (S08 & S09), the left parietal (S04), or the medial occipital or occipito-temporal electrode sites (S02, S03, S05 & S10).

3.3.4. Face discrimination response: Greyscale vs. contrast-reversed

SNR at the frequencies related to oddball face discrimination was largely reduced in the contrast-reversed compared to the greyscale condition (Fig. 8B; Fig. 9). The mean SNR of common significant harmonics between conditions (i.e., 1.18 Hz, 3.53 Hz, and 4.70 Hz) in the rOT ROI revealed significantly higher responses for greyscale than for contrast-reversed faces ($t(8)=3.88$, $p<0.002$; Fig. 8D). This difference was restricted to the face discrimination frequencies, since responses were equivalent at

the base stimulation frequency. This pattern of results was present in all participants (Table 2). In this second experiment, we also did not find significant correlations between the 1.18 Hz oddball response and the 5.88 Hz base response in the rOT (greyscale: $r=-0.22$, $p=0.56$; contrast-reversed: $r=-0.05$, $p=0.90$) nor between the oddball response in the rOT and the base response in the medial occipital ROI (greyscale: $r=-0.36$, $p=0.34$; contrast-reversed: $r=-0.07$, $p=0.86$).

4. Discussion

4.1. Summary and advantages of the approach

Our two experiments demonstrated that fast periodic oddball stimulation can index high-level face discrimination. Robust measures of individual face discrimination were obtained at the exact frequency at which the oddball face identity changes were introduced (every 850 ms, or 1.18 Hz) and at its harmonics. The discrimination response was present in every participant in our study, despite recording for only a few minutes. The largest and most consistent responses were localized over the right occipito-temporal cortex, in line with the known neurofunctional basis of face perception (e.g., Sergent et al., 1992; Bouvier & Engel, 2006) and of face-sensitive event-related potentials (ERPs) to transient stimulation (e.g., N170, Bentin, McCarthy, Perez, Puce, & Allison, 1996; Rossion & Jacques, 2011 for a review).

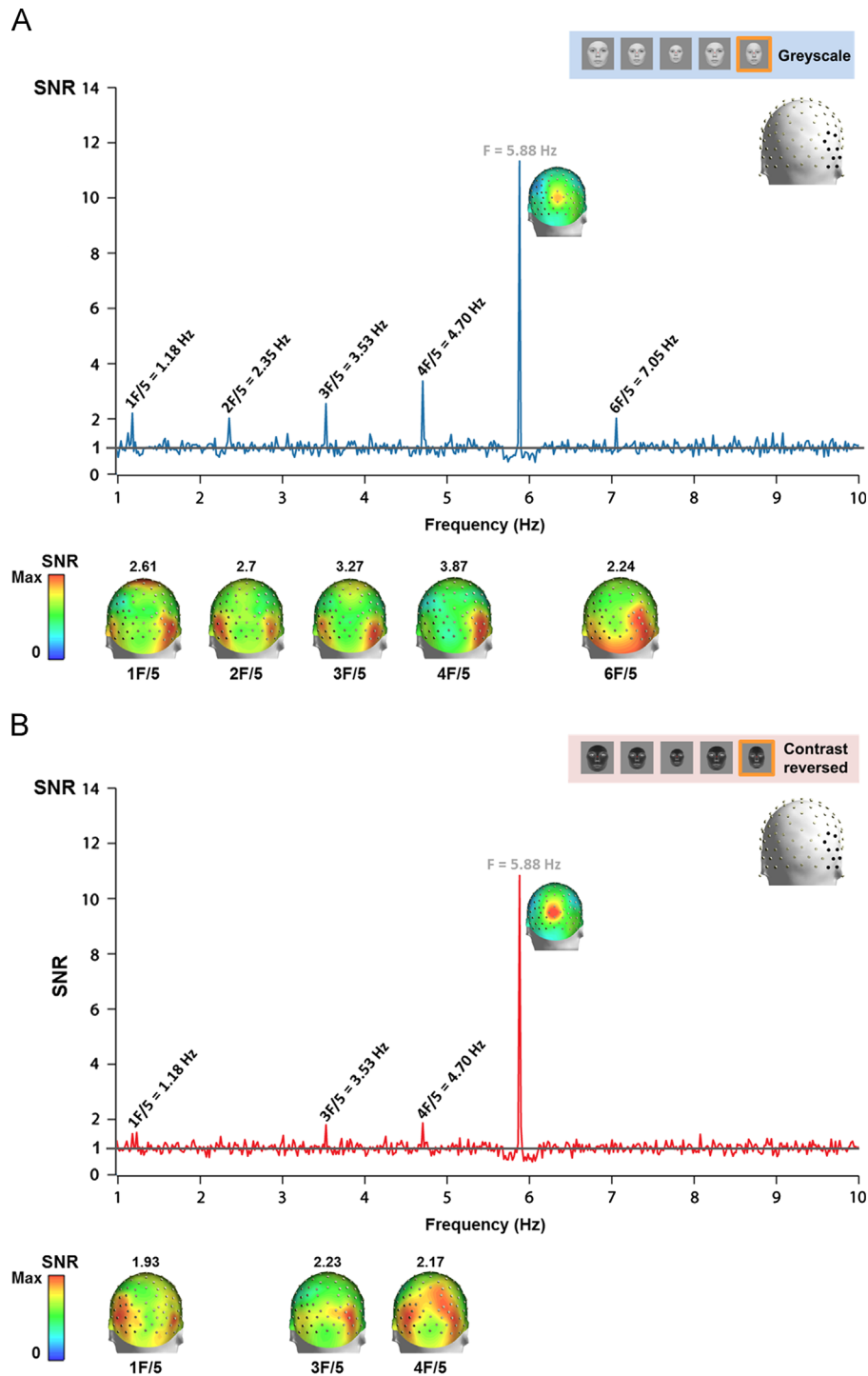


Fig. 9. SNR spectra of the right occipito-temporal ROI in Experiment 2. The channels composing this ROI are indicated with black dots on the blank 3D head in the upper right. On the SNR spectra, only significant peaks (Z -score > 1.96) are labeled. Below the spectra, 3D topographies of each harmonic are shown at their individual color scales (the scales' maxima are shown above each topography). (A) In the greyscale condition, all the responses related to face discrimination were clearly defined and significant, from the fundamental frequency (1.18 Hz) until its 6th harmonic (7.05 Hz). All topographical maps showed larger responses over the occipito-temporal regions, with a clear right hemisphere lateralization. (B) For contrast-reversed faces, not only were there fewer significant responses, but these were also of smaller magnitude. Contrary to greyscale faces, there was no clear right lateralization.

Although the fast periodic oddball paradigm is not optimized to identify successive responses in the time domain, this approach, and fast periodic visual stimulation in general, has a number of significant advantages compared to classical ERP experiments. First, periodic stimulation provides an *objective* signature of the neural process of interest, in this case individual face discrimination. This is because the experimenter defines the frequency of the stimulation *a priori*, so that the EEG signal at this frequency is intrinsically meaningful and

distinguishable from the irrelevant noise randomly distributed in other frequency bins. If a sufficiently long stimulation sequence is used, the resulting high frequency resolution concentrates all the response of interest in a very narrow frequency band compared to the total EEG bandwidth. A very high SNR can be obtained this way (Regan, 1989), even for short acquisition periods: oddball responses were significant even in a single 1-min trial. To our knowledge, there are no other approaches that can provide such a robust neural marker

of visual discrimination in such a short time-scale. Furthermore, responses can be obtained implicitly, i.e. while participants complete an entirely orthogonal task and are unaware of the experimental manipulation. This opens the possibility of using the approach with participants who are unable to provide explicit discrimination responses due to decisional, motor or cognitive limitations, such as patients or infants.

Many of these advantages have been described in recent EEG studies using fast periodic stimulation with faces (Rossion & Boremanse, 2011; Rossion et al., 2012); however, the most important advantage specific to the periodic oddball paradigm is its ability to isolate a discrimination response without relying on a subtractive operation between separately recorded conditions. Instead, a periodic response at the oddball frequency is a measure of a difference in response magnitude to the base and oddball stimuli. Hence, a significant signal at the oddball frequency is sufficient in itself to infer discrimination. This method is flexible, since the experimenter can easily manipulate the dimension and the finesse of the discrimination by varying the nature of the base and oddball stimuli. Moreover, the different behavior of the base and oddball frequencies across conditions and their differences in scalp topography (medial occipital for the 5.88 Hz base frequency and right occipito-temporal for the 1.18 Hz oddball frequency) imply that these responses reflect distinct processes: one related to individual face discrimination (oddball frequency) and the other the general responsiveness of the system to visual pattern stimulation (base stimulation frequency)².

4.2. Excluding attentional and low-level confounds

Although the steady-state responses elicited by periodic stimulation are sensitive to attention (e.g., Morgan, Hansen, & Hillyard, 1996; Keil, Moratti, Sabatinelli, Bradley, & Lang, 2005; Müller et al., 2006), the individual face discrimination response obtained here cannot be generated by attentional processes. First, because participants performed a neutral color change detection task, they were unaware of periodic face changes (although they reported noticing different faces, none reported seeing *periodic* face changes). Moreover, the effects of voluntary attentional orientation on steady-state amplitude are relatively slow (≈ 750 ms in Kashiwase, Matsumiya, Kuriki, & Shioiri, 2012) and would predict at least a four-cycle delay in the time-domain, in contrast to the small 1-cycle delay observed here. Finally, differences between conditions at the face discrimination frequency cannot be due to global attentional differences, because these would have also affected EEG amplitude at the base stimulation frequency (e.g., Pei, Pettet, & Norcia, 2002; Chen, Seth, Gally, & Edelman, 2003; Müller et al., 2006; Wang, Clementz, & Keil, 2007; Hönegger et al., 2011). Yet, these 5.88 Hz responses did not differ between conditions.

Evidence against low-level visual confounds stems from three arguments. First, oddball responses were observed despite large stimulus size changes at every stimulation cycle, excluding effects of pixelwise or retinotopic discrimination. Relative size-invariance of responses is characteristic of high-level object and face-sensitive regions (Grill-Spector et al., 1999; Sawamura, Georgieva, Vogels, Vanduffel, and Orban, 2005). Second, the highest response related to individual face discrimination was systematically clustered around occipito-temporal channels, with a

strong right hemisphere lateralization. Across both studies, mean oddball responses were significantly larger in the occipito-temporal region on the right than the left ($t(19)=2.341$, $p < 0.015$, one-tailed). Such scalp topographies are similar to those of the face-related N170 component found in ERP studies, which reflect high-level visual processes and face individualization in particular (Bentin et al., 1996; Jacques et al., 2007; for reviews see Eimer, 2011; Rossion & Jacques, 2011). The phase reversal of the response on central channels compared to occipito-temporal channels also resembles the relationship between the N170 and its positive counterpart on the vertex, the vertex-positive potential (VPP, Jeffreys, 1996; Joyce & Rossion, 2005). Additionally, previous block design periodic visual stimulation studies at lower frequencies have all shown face discrimination activity peaking at similar electrode sites (Rossion & Boremanse, 2011; Rossion et al., 2012; Prieto et al., *In press*). Finally, and most importantly, we observed a significant reduction of the discrimination response with upside-down or contrast-reversed stimuli, two manipulations that preserve low-level differences between individual faces. This observation demonstrates for the first time that oddball responses as captured during fast periodic stimulation can reflect high-level visual processes.

4.3. Effects of inversion, contrast-reversal, and color

The decreased individual face discrimination response due to inversion and contrast-reversal is in line with behavioral studies. Both these well-documented manipulations are known to hinder individual face perception. While inversion primarily disrupts the processing of shape and relative distances between features (Yin, 1969; Freire et al., 2000; see Rossion, 2009 for review), contrast-reversal degrades surfaces cues (Galper, 1970; Bruce & Langton, 1994; Kemp, Pike, White, & Musselman, 1996; Russell et al., 2006). Above all, these two conditions reveal complementary face-specific effects (Yin, 1969; Biederman & Kalocsa, 1997; Nederhouser et al., 2007), so that the observed reduction in discrimination response is probably linked to the disruption of high-level face identity perception.

To a lesser degree, the elimination of color information in our second experiment also affected face discrimination (i.e. there were fewer significant harmonic responses, see Fig. 3). Although less salient than face shape, color also plays an important role in face individualization (Troje & Bülthoff, 1996; Lee & Perrett, 2000; Yip & Sinha, 2002). More specifically, color appears especially important when viewing conditions are degraded (e.g., through blurring in Yip & Sinha, 2002). The fast presentation rate and face size changes in our experiment could have decreased discrimination efficiency. However, a direct comparison between the color and greyscale faces did not reveal any significant differences either in the magnitude of the response ($t(18)=0.66$, $p=0.26$) or in the number of oddball harmonics ($t(18)=0.56$, $p=0.29$). The results thus underline the robustness of the oddball even in the context of impoverished face identity information.

4.4. Neuro-functional basis of the periodic oddball response

As mentioned above, the right occipito-temporal topography of the oddball face discrimination response is typical of face-sensitive potentials such as the N170 (Bentin et al., 1996; George, Evans, Fiori, Davidoff, & Renault, 1996; Eimer, 2011; Rossion & Jacques, 2011), and is in line with the right hemisphere dominance for face perception (e.g. Hécaen & Angelergues, 1962; Sergent et al., 1992). The visual areas involved in face perception are widely distributed (Sergent et al., 1992; Allison, Puce, Spencer, & McCarthy, 1999; Haxby et al., 2000; Weiner & Grill-Spector, 2012; Rossion et al., 2012) and many if not all of them potentially mediate individual

² Note that there is a caveat to such a functional subdivision of the two frequency responses in that the base response is also the 5th harmonic of the oddball response ($5 \times 1.18 \text{ Hz} = 5.88 \text{ Hz}$), and thus, also reflects discrimination to some degree. However, the question of whether the base frequency is a pure measure of low-level processing is irrelevant to the interpretation of the oddball frequency, which is a pure measure of discrimination thanks to the experimental design.

face discrimination (e.g., Gauthier et al., 2000; Andrews & Ewbank, 2004; Davies-Thompson et al., 2009). Several cortical sources in the ventral and lateral occipito-temporal cortex could thus contribute to the discrimination responses measured with our paradigm.

Although the periodic oddball response shares similarities with the face-sensitive ERP components, they are not equivalent. At the conceptual level, the oddball response can be likened to a N170 amplitude difference between different and same faces, as demonstrated in several studies (e.g., Jacques et al., 2007). However, it could also reflect individual face discrimination responses as observed on later components (e.g., N250r; Schweinberger, Huddy, & Burton, 2004). More generally, this conceptual similarity does not imply that the periodic responses are juxtapositions of N170 components or other components. The exact relationship between periodic EEG responses (“steady-state evoked potentials”) and transient ERP components is still a matter of debate (Regan, 1989; see Rossion & Boremanse, 2011 and Rossion et al., 2012 for a more in depth discussion of this issue for face-related responses). It has been claimed that steady-state evoked potentials can be fully accounted for by linear superposition of ERP components (Galambos, Makeig, & Talmachoff, 1981; Capilla, Pazo-Alvarez, Darriba, Campo, & Gross, 2011). However, this claim is controversial, and drawn from responses to low-level stimuli such as click sounds or contrast-reversing checkerboards. Whether this interpretation can be generalized to complex high-level visual responses such as those investigated here remains an open question.

The potential neural mechanisms that generate the periodic oddball face discrimination response could be similar to those underlying the mismatch negativity response in the auditory (MMN, Näätänen, Gaillard, & Mäntysalo, 1978) and visual domains (Pazo-Alvarez, Cadaveira, & Amenedo, 2003). Several accounts of the MMN have been proposed: change detection, adaptation, model adjustment, novelty detection, and prediction error (Leider, Daunizeau, Garrido, Friston, & Stephan, 2013; see also Winkler, 2007; Kimura, Schröger, & Czigler, 2011). While change detection and adaptation models describe the MMN based on the computation of relative differences between base and oddball stimuli, the three other models describe the MMN in a broader, prediction-based framework. Based on what is known about the discrimination of the specific visual category used here, i.e., faces, the neural mechanisms that underlie the oddball response could be due to different subgroups of neurons within the same population responding to the repeated base face compared to the periodically introduced different oddball faces (e.g., Young & Yamane, 1992; Abbott, Rolls, & Tovee, 1996; Leopold, Rhodes, Müller, & Jeffery, 2005; Freiwald et al., 2009). These two types of responses can be distinguished at a larger scale on the scalp only if the amplitude of the periodic response at the rate of face change (1.18 Hz) differs from that of the responses at the base stimulation frequency (5.88 Hz) (Fig. 6). We propose that this differentiation arises from a release from repetition suppression of the base face every time different oddball faces are shown³. Similar to our previous studies using fast periodic visual stimulation (Rossion & Boremanse, 2011; Rossion et al., 2012; Prieto et al., *In press*), the fast periodic oddball paradigm probably shares the same neural mechanisms of classic repetition suppression paradigms (Henson, 2003; Grill-Spector et al., 1999; Jacques et al., 2007), but with the

advantages of increased objectivity, sensitivity and direct isolation of the differential response of interest.

4.5. Oddball frequency harmonics

In both experiments, we observed significant responses at the oddball frequency (1.18 Hz) as well at its harmonics (2.35 Hz, 3.53 Hz...). Although the response was present at the fundamental oddball frequency, the largest SNR were obtained on the higher harmonics (3.53 Hz in Experiment 1 and 4.70 Hz in Experiment 2). There are several possible explanations for this response pattern. First, the appearance-disappearance pattern of oddball stimuli within the base stimulus sequence can be conceptualized as a 1.18 Hz square-wave presentation with a 20% duty cycle (1 oddball for every 5 base stimuli = $1/5 = 20\%$). This unequal duty cycle will result in odd and even harmonics in addition to the fundamental frequency. Second, the brain does not process even perfectly sinusoidal stimulation in a linear manner, so that responses at harmonic frequencies are to be expected (Regan, 1989). Furthermore, the optimal frequency band of the discrimination response may be tuned higher than the current oddball frequency (1.18 Hz). This could be tested in future studies by keeping the current base frequency and varying the interval of the oddballs (i.e. 1/3 instead of 1/5). Finally, another reason for the reduced fundamental oddball response is the $1/F$ distribution of the human EEG spectrum. Noise is highest in the lowest frequency bands so that the signal-to-noise ratio of 1.18 Hz appears smaller than other harmonics, but it does imply that the absolute magnitude at this frequency is necessarily smaller (this is especially the case in Experiment 1, see [Supplementary figure and table](#)). In summary, there are properties related to the stimulation, to the EEG noise, and to the non-linearity of the neural response that could have contributed to the pattern of harmonic responses seen here. However, despite this issue, all these harmonic responses should be considered as reflecting a discrimination of the oddball from the base face stimulus.

4.6. Conclusions and perspectives

In addition to providing an objective measurement of high-level discrimination with a high SNR and with a single measurement, rather than a difference between two measurements, the fast periodic oddball method is very efficient (robust responses can be acquired in a few minutes of experiment) and behavior-free, requiring no explicit task to process facial identity. The low attentional task demands of this paradigm also make it particularly well suited to work with difficult-to-test populations such as infants, young children or brain-damaged patients, especially since reliable responses can be obtained in individuals in just a few trials. In future studies, it would be interesting to explore how these implicit oddball discrimination responses relate to other neurofunctional and behavioral measurements of face discrimination, and to interindividual face processing abilities in general (Bowles et al., 2009; Wilmer et al., 2010). Another issue worth investigating is whether the implicit oddball response is modulated by the task-relevance of the oddball faces (i.e., explicit vs. implicit attention to periodic changes of face identity).

We chose to use faces as stimuli in the current experiment because they are a visually homogenous set of highly familiar stimuli that are associated with well-defined neural responses. Moreover, unlike other object categories, faces need to be processed beyond a simple category-wise classification (“it’s a face”) into fine-grained subordinate-level discrimination (“it’s face X, not face Y”) in order to ensure adequate social interactions. This allowed us to validate the paradigm in an extreme case of individual discrimination. However, this technique could easily

³ Note that even if unspecific prediction-based mechanisms were involved, the clear dissociation between stimulus conditions (i.e., upright vs. inverted and greyscale vs. contrast-reversed) implies that high-level face discrimination processes were necessarily implicated in generating the predictions and prediction errors.

be applied to measure the properties of other face categorization processes (e.g., face detection, facial expression coding, familiar face recognition...) or to examine the neural representation of a variety of complex visual stimuli, such as objects or scenes.

Future studies will be necessary to establish the limitations and optimal parameters of the fast periodic oddball paradigm for different types of experiments. The oddball sequence is defined by both the base frequency of stimulation and the frequency of presentation of the oddball stimuli. Both these values could be used to refine the fast periodic oddball approach. For instance, we stimulated at a base rate of 5.88 Hz in this study since previous research in the lab indicated that this was optimal frequency rate to examine face individualization effects in block designs (Prieto et al., *In press*). At this frequency, the visual system is able to detect differences with previous face stimuli presented with a SOA of 170 ms, before the next stimulus could potentially act as a mask. At higher frequency rates, the delay between successive faces could potentially exceed the speed of face individualization processes. In contrast, at lower frequency rates, response to the oddball faces could be more dispersed and include processes beyond individual discrimination. In future studies, it is also possible that fewer than four base stimuli in between the oddball stimulus may be used to generate reliable periodic oddball responses. Finally, we have used 1-min sequences as a compromise between good frequency resolution and reasonable testing time. It is possible that other stimulation frequencies could lead to even shorter stimulation durations, thus further improving the efficiency of this approach.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2013.10.022>.

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