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Original Article

ORIGINAL ARTICLE

At a Single Glance: Fast Periodic Visual Stimulation Uncovers the Spatio-Temporal Dynamics of Brief Facial Expression Changes in the Human Brain

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Abstract

Detecting brief changes of facial expression is vital for social communication. Yet, how reliably, how fast these changes are detected and how long they are processed in the human brain remain unknown. High-density electroencephalogram (EEG) was recorded in 18 participants presented with a neutral-expression face at a rate of 5.88 Hz (*F*) for 80 s. Every five faces, the face changed expression to fear, disgust or happiness (different stimulation sequences). The resulting 1.18 Hz (*F*/5) EEG response and its harmonics objectively indexed detection of a brief change of facial expression. This response was recorded in every participant in a few minutes but was largely reduced for inverted faces, indicating that it reflects high-level processes. Although this response focused on occipito-temporal sites, different expression changes evoked reliably distinct topographical maps, pointing to partly distinct neural generators. These effects were also observed at a faster 12 Hz frequency rate and a lower ratio of expression change (1/9). Time-domain analysis showed that a brief change of expression inserted in a dynamic stimulation sequence elicits specific occipito-temporal responses between 100 and 310 ms, indicating a rapid change detection process followed by a long integration period of facial expression information in the human brain.

Key words: EEG, FPVS, facial expressions, oddball paradigm

Introduction

Human faces provide a wealth of information—identity, age, gender, emotional state and, possibly, enough information to infer intentions. Being able to quickly read this information, especially emotional expression, is vital for social interactions and even survival (Darwin 1872). In particular, 6 facial expressions—fear, disgust, sadness, happiness, anger, and surprise—also known as the *basic emotions* (Ekman 1993) have been suggested to be effectively transmitted and decoded (Smith et al. 2005), and thus universally recognized (for a meta-analysis, Elfenbein and Ambady 2002). However, despite a wealth of research on human processing of facial expressions (e.g. Ekman 1993; Adolphs 2002; Brosch et al. 2009), our understanding of how well and how fast the human brain detects a *brief* facial expression change, i.e. from a neutral face to an expressive face, and *how long* this novel expression is processed, remains limited.

Despite the efficient processing of facial expressions, a common finding of behavioral studies is that some facial expressions (e.g. fear, disgust, sadness) are often misclassified (Palermo and Coltheart 2004; Calvo and Lundqvist 2008; Campbell and Burke 2009). Moreover, correct categorization of these expressions drops with short presentation times (e.g. Calvo and Lundqvist 2008, Neath and Itier 2014). For example, poor identification of facial expressions is observed when backward-masked images are presented for a duration less than 20 ms, with a gradual improvement for longer presentations (e.g. Calvo and Lundqvist 2008; Milders et al. 2008;

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Neath and Itier 2014). Yet, response times and accuracy data in explicit judgments of facial expressions reflect only the output of the system. Thus, these variables can be greatly influenced by decisional factors and do not provide clear information regarding the ability of the human brain to detect brief changes of facial expression. Moreover, behavioral studies are limited to provide information about the speed at which these changes are detected, how long they are processed, and whether the responses to brief expression changes vary in intensity for various categories of expressions.

One approach to clarify these issues is to measure facial expression processing without an explicit behavioral task, using neurophysiological measures such as event-related potentials (ERPs, Luck 2005), which, thanks to their excellent temporal resolution, may provide information about the speed and time course of facial expression processing. In standard ERP studies, images of expressive faces are presented foveally for relatively long periods of time, ranging from 200–300 ms (e.g. Eimer and Holmes 2002; Blau et al. 2007; Wronka and Walentowska 2011), to 1000 ms (Schupp et al. 2004; Caharel et al. 2005; Rellecke et al. 2012; Smith et al. 2013). The expressive face is typically followed by a blank screen of a variable duration during which further processing of all aspects of the stimulus, not just the change of expression, can continue. In these conditions, facial expressions modulate ERP components ranging in a time window of 100 ms up to 1000 ms post-stimulus onset (Eimer and Holmes 2007).

In general, while early components (i.e. 100–250 ms post-stimulus presentation) are proposed to carry information about differences between expressive and neutral faces (e.g. Batty and Taylor 2003; Caharel et al. 2005; Wronka and Walentowska 2011), the subsequent components (i.e. after 250 ms post-stimulus) appear to differentiate among expressions (e.g. Luo et al. 2010; Rellecke et al. 2012, 2013). Even though the early effects (~100 ms post-stimulus) are often attributed to rapid attentional processing of expressive faces (Batty and Taylor 2003; Santesso et al. 2008; Wronka and Walentowska 2011), low-level information in the images, which is generally uncontrolled in these studies, can also account for differential amplitudes of these components between expressive and neutral faces (e.g. Johannes et al. 1995). As for the modulations of the late ERP components, they are contingent on the task type or attention allocation to the expressive faces (e.g. Krolak-Salmon et al. 2001; Eimer and Holmes 2002, Eimer et al. 2003; Wronka and Walentowska 2011). More generally, it is fair to say that the modulation of ERP waveforms by facial expressions is relatively weak. Hence, it is usually not revealed at the individual subject level, and largely inconsistent across studies, in line with the conclusions of a recent review on the topic "…the major conclusion that can be drawn from electrocortical research is that, between 150 and 300 ms (i.e. the N170 to EPN latency range), emotional expression is implicitly encoded as different from neutral expression, followed by some discrimination among the emotional faces, albeit no solid and systematic pattern has emerged" (Calvo and Nummenmaa 2015).

This discrepancy in results across studies is not that surprising since ERPs recorded on the scalp reflect brain activation at a system level of organization. Hence, unless different expressive faces are coded by populations of neurons in widely separated brain areas, there is no reason to expect consistent differences in the absolute amplitude of an ERP component when neutral or expressive faces are contrasted against a no-stimulus baseline (Rossion 2014). To circumvent this issue and measure a contrast between neutral and expressive faces, more recent ERP studies employ a paradigm in which a deviant (expressive) "oddball" face is presented in a stream of "standards" (neutral) face images. The component elicited by the oddball stimuli has been defined as a visual mismatch negativity (vMMN), arising when the oddball input mismatches a common and expected representation formed by the preceding stimulus sequence (Stefanics et al. 2011; Kimura et al. 2011). Since the vMMN is a change detection component, this type of paradigm is potentially better tailored at detecting *changes* of expression, measuring the differential response to expressive faces in comparison to other images rather than the general or absolute response of the system to facial images with various emotional expressions. Yet, even though the vMMN is observed around 200–400 ms post-stimulus onset over parieto-occipital and occipito-temporal and more rarely over fronto-central sites (Kimura et al. 2011), it is also highly variable across individuals and studies, making it difficult and somewhat subjective to define the presence of a vMMN and quantify it in individual participants. As an illustration of the low consistency across studies, vMMN to happy expression compared to neutral images has been reported at various time windows: 110–360 ms (Zhao and Li 2006), 120–220 and 220–320 ms (Chang et al. 2010), and 150–180 and 280–320 ms (Astikainen and Hietanen 2009) over occipito-temporal sites. This low consistency is partly due to the low signal-to-noise ratio (SNR) of standard ERP measures, exacerbated by the low frequency of oddball stimuli (i.e. 10–20%), requiring averages of many trials from a long recording duration to obtain typical responses.

Finally, and most importantly for the goal of the present study, in typical oddball paradigms generating the vMMN component, although face stimuli are presented for short durations (e.g. 100–200 ms), they are not backward-masked, and inter-stimuli intervals are fairly long—at least 300 ms (Zhao and Li 2006) but more often about 500 ms (e.g. Astikainen and Hietanen 2009; Li et al. 2012; Stefanics et al. 2012; Astikainen et al. 2013) which allows further processing of all aspects of the stimuli. Thus, despite their high interest, these studies do not measure the human brain's detection of brief changes of facial expression, do not provide information about how fast these changes are detected and how long they are processed, and whether the responses to brief expression changes vary in intensity and spatio-temporal signatures for various categories of expressions.

Here we addressed these outstanding issues using a recently developed approach termed Fast Periodic Visual Stimulation (FPVS, Rossion 2014) in electroencephalography (EEG). FPVS is based on the long-standing observation that the human brain synchronizes its activity to the periodic rate of a flickering stimulus (Adrian and Matthews 1934) a periodic response that has been defined as a "Steady-State Visual Evoked Potential" (SSVEP, Regan 1966; Norcia et al. 2015 for a review). Traditional SSVEP research consists in repeating the exact same stimulus, usually a low-level visual stimulus (gratings, luminance flicker, etc.) or even a complex image such as an expressive face (e.g., Wieser and Keil 2014) at a high frequency rate (i.e., 10 Hz or above). Most recently, Rossion and Boremanse (2011) showed that changing a high-level visual property, i.e. face identity, at a rapid periodic frequency of stimulation (3–9 Hz, Alonso-Prieto et al. 2013), allows measuring the response of the system to this property with great sensitivity by concentrating all of the response at this specific stimulation frequency rate. The term "FPVS" is preferred here to the term "SSVEP" because FPVS refers to the approach rather than the type of EEG response

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expected (Rossion, 2014). Even though is is widely used, the term SSVEP is loaded and more ambiguous, since there are different definitions of what is a SSVEP as opposed to a standard ERP response (e.g., Regan 1966; Heinrich 2010; Norcia et al. 2015). Here we do not make any assumption regarding the type of EEG response targeted and obtained. Moreover, with frequency rates between 3 and 9 Hz, adaptation decreases the "steadiness" of the periodic EEG response to complex stimuli such as faces (Rossion and Boremanse 2011; Nemrodov et al. 2015), so that using the term "SSVEP" in the context of repeated stimuli as used here does not seem fully appropriate. In the most recent studies, this approach has been extended to a fast periodic "oddball" stimulation sequence in which a deviant face stimulus is introduced periodically within a sequence of standard stimuli presented at a fast periodic rate (Liu-Shuang et al. 2014). The deviant stimuli elicit a response measurable in the frequency domain if and only if they are discriminated from the base stimuli and provide a common (i.e. generalized) discrimination response. This oddball FPVS approach has demonstrated its sensitivity to high-level visual processes in adults, in particular for discrimination of different facial identities (Liu-Shuang et al. 2014; Dzhelyova and Rossion 2014a; 2014b).

Compared to a more traditional ERP approach, the FPVS-EEG oddball paradigm provides a robust visual discrimination response that can be identified objectively (i.e. at an experimentally predefined frequency), quantified directly, and without post hoc comparison—i.e. subtraction—of a response evoked by a standard and a deviant stimulus as in the vMMN approach. Moreover, the base stimulation rate can be quite fast —typically about 6 faces/s—allowing the collection of many discriminative responses in a short amount of time, and putting the system under tight temporal constraints: a change of facial expression, as measured in the present study, appears for less than 170 ms, in between 2 neutral faces that act as forward and backward masks (Alonso-Prieto et al. 2013; see Fig. 1 and Supplementary Movies 1–3 here). This duration corresponds to one gaze fixation maximum, testing for the discrimination of brief changes of facial expression at a single glance. All of these characteristics make this approach potentially invaluable to define and quantify the human brain's sensitivity to detect brief changes of facial expressions, as well as the spatio-temporal signature of this detection from neutral faces for various expressive changes: here, happy, fearful, and disgusted faces.

Experiment 1

Methods

Participants

Eighteen participants (7 males, mean age = 23.16, SD = 3.36, range = 20–35, all right-handed) provided signed and informed consent and were paid for their participation in the experiment, which was approved by the ethical committee of the University of Louvain. They reported normal or corrected-to-normal vision. None of the participants reported any history of psychiatric or neurological disorders.

Stimuli

Eight individuals (4 males) from the Karolinska Directed Emotional Faces (AF01, AF11, AF15, AF29, AM01, AM06, AM14, AM35, Lundqvist et al. 1998) were selected. For each individual, a neutral expression and the corresponding fearful, disgusted, and happy expressions in full front images were used. These expressions were chosen due to their high evolutionary significance and key role in motivating behavior (e.g. Marsh et al. 2007; Shariff and Tracy 2011; Tybur et al. 2013). The background of the images was replaced by a gray color (128/255, 128/255, 128/255). Image size was set to a height of 210 pixels × 290 pixels, 5.48° and 6.90° at 1 m viewing distance. Mean pixel luminance of the faces, excluding the pixels defined as the background mask, was equalized during stimulus presentation.

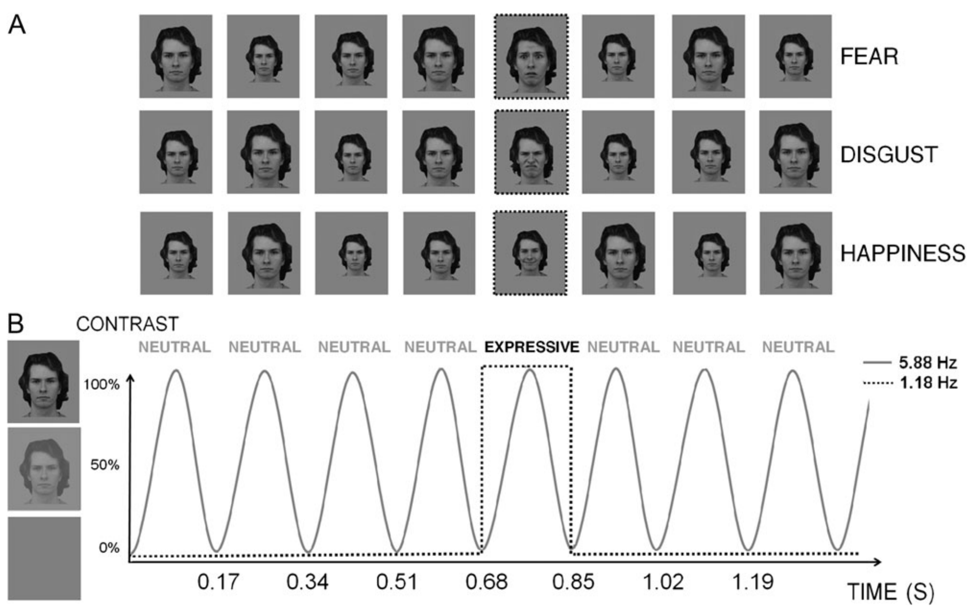

Figure 1. Experimental design. (A) Facial stimuli: neutrally expressive faces are presented sequentially at a fast rate (5.88 Hz, 170 ms stimulus onset asynchrony (SOA), 1 fixation/face) with every fifth face being an expressive face (same identity), displaying one of the emotions (fear, disgust, happiness). A stimulation sequence lasts 84 s (80 s stimulation and 2 s of fade in and fade out). (B) Stimulation: as in previous studies (e.g. Liu-Shuang et al. 2014), faces are sinusoidally contrast-modulated over time at the rate of 5.88 Hz. Note that there are 2 embedded frequencies: 5.88 Hz—base frequency and 1.18 Hz—oddball frequency.

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Procedure

The procedure was similar to a recently reported study with a fast periodic oddball paradigm on face identity (Dzhelyova and Rossion 2014a). The number of conditions is 6: 2 orientations (upright or inverted) and 3 emotional expressions (fear, disgust, and happiness). Each condition was repeated only 4 times (2 female and 2 male identities), resulting in 24 sequences. The choice of identities for each sequence was counterbalanced across participants. For each sequence one individual with a neutral expression (base face) was selected and the corresponding image with one of the emotional expressions was used as an oddball stimulus. Each sequence started with a variable duration of 2–5 s of a blank screen, 2 s of gradually fading in of the stimuli presentation, followed by 80 s of stimulation sequence and 2 s of gradually fading out of the stimuli. Sequence order was randomized. To avoid low-level repetition effects, the size of the images was randomly varied between 90% and 110% (4.93° and 6.21°, and 6.28° and 7.58° of visual angle, respectively, for the 2 extreme cases) at every stimulation cycle. When tested for face identity changes, this 20% image size change gives rise to a large oddball response that is not contaminated by low-level visual cues (Dzhelyova and Rossion 2014b). In addition to the size change variation, to minimize low-level effects, we included a control condition in which we presented inverted faces. Inversion preserves image-based cues but impairs high-level (rapid) processing of faces, including facial expression processing (e.g. Prkachin 2003; Calvo and Nummenmaa 2008; Derntl et al. 2009; Bombari et al. 2013).

The stimuli were presented on a CRT 17-in. (43-cm) monitor controlled by a computer. The facial images were displayed at a rate of 5.88 Hz (i.e. 5.88 images/s) with the constraint that every fifth face, the same individual but with an emotional expression (e.g. happy A_{happy}) was presented, thus resulting in a sequence $A_{neutral}A_{neutral}A_{neutral}A_{neutral}\boldsymbol{A_{happy}}$ $A_{neutral}A_{neutral}A_{neutral}A_{neutral}\boldsymbol{A_{happy}}$ (see also Fig. 1; Supplementary Movies 1–3). Images were presented through sinusoidal contrast modulation (0–100%) using Psychtoolbox 3.0.9 for Windows in Matlab 7.6 (MathWorks Inc.) (e.g. Liu-Shuang et al. 2014; see Fig. 1). Thus, each pixel of the images reached the full luminance value of the face stimulus after half a cycle, approximately 85 ms after stimulus onset ((1000/5.88)/2). A practical advantage of the sine mode of stimulation is that it is a smoother stimulation mode than square wave stimulation and it is defined with a single parameter (stimulus onset asynchrony (SOA) or rate). Another advantage is that the visual stimulation is present almost all the time, thus giving a continuously changing percept.

To measure the discrimination response to emotional expression, only frequencies corresponding to the frequency when the expressive faces appeared were considered, namely 5.88 Hz/5 = 1.175 Hz, rounded to 1.18 Hz. As a result, EEG amplitude at precisely this frequency (F/5 = 1.18 Hz—the oddball frequency) and its harmonics (i.e. 2F/5 = 2.352 Hz, 3F/5 = 3.528 Hz, 4F/5 = 4.704 Hz, rounded to 2.35 Hz, 3.53 Hz, and 4.70 Hz, respectively) was used as an index of emotional expression discrimination.

Participants were seated in a dimly lit room with 1 m viewing distance to the screen. They were instructed to respond when they noticed a color change of the fixation cross. The fixation cross was presented in the center of the face stimuli, just below the eyes and briefly (300 ms) changed color from black to red 10 times within every sequence. This orthogonal task guaranteed that the respondents were attentive. At the end of the experiment, participants were asked to complete a short questionnaire, examining if they noticed anything about the faces and if so to specify what it was. Although everyone except one participant noticed that expressive faces appeared during the stimulation, they did not realize that the change of expression happened periodically.

Complementary Behavioral Experiment (Explicit Detection of Changes of Expression)

In order to ensure that participants were able to explicitly recognize the changes of expression despite the relatively fast presentation of the stimuli, a behavioral task was performed after the completion of the EEG recording. In this complementary experiment, participants had to explicitly detect each change of the facial expression (e.g. neutral to happy), which appeared non-periodically, 20 times in total during each 84 s sequence. Similarly to the EEG experiment, faces were presented at 5.88 Hz and in each sequence the oddball faces displayed only one of the expressions (fear, disgust, or happiness).

EEG Acquisition

Electroencephalographic (EEG) activity was recorded using a BIOSEMI Active-Two (common mode sense active electrode and driven right leg passive electrode) amplifier system with 128 Ag/AgCl electrodes. Vertical eye movements were recorded with 2 electrodes positioned above and below the right eye. Horizontal eye movements were recorded with electrodes placed at the corner of each eye. EEG and electrooculogram recordings were sampled at 512 Hz.

EEG Analysis

Preprocessing. All EEG processing steps were carried out using Letswave 5 (http://nocions. webnode.com/letswave), and Matlab 2012 (The Mathworks). The continuously recorded data were cropped into 86-s segments (4 s before and 2 s after each stimulation sequence) and was then bandpass filtered at 0.1–100 Hz (Butterworth filter, fourth order). The data were then resampled to 250 Hz to save disk space and reduce computational load. For 3 participants who blinked on average above 0.44 times/s (average number of blinks across participants = 0.13, SD = 0.16), blinks were corrected by means of independent component analysis (ICA) using the runica algorithm (Bell and Sejnowski 1995; Makeig et al. 1996), as implemented in EEGLAB. This algorithm outputs a square mixing matrix in which the number of components corresponds to the number of channels. For each of these 3 participants, only the first component, accounting for most of the variance, representing vertical eye movements was removed. Next, noisy or artifact-ridden channels were re-estimated using linear interpolation of the 3 nearest spatially neighboring electrodes (not more than 5% of the electrodes, on average across participants 1.3 electrodes were interpolated). All data segments were re-referenced to a common average reference.

Frequency-domain analysis. Preprocessed data segments were cropped down to an integer number of 1.18 Hz cycles beginning immediately after the fade in, until approximately 81.94 s (~80 s, 94 cycles, 19986 time bins in total). Data were averaged in the time domain, separately for every condition: *Orientation* (Upright; Inverted) and *Facial Expression* (Fear; Disgust; Happiness) for each participant. A fast fourier transformation (FFT) was then applied to these averaged segments and amplitude spectra were extracted for all channels.

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The FFT transformation yielded a spectrum ranging from 0 to 250 Hz with a high spectral resolution of about 1/80 s, i.e. 0.0125 Hz.

To assess the significance of the responses at different harmonics, Z-scores were calculated on the FFT grand-averaged data pooled across all electrodes for each condition. Z-scores were computed as in previous studies, using the mean and standard deviation of the 20 frequency bins surrounding the frequency of interest (excluding the immediately neighboring bin and the 2 most extreme values, e.g. Liu-Shuang et al. 2014). Harmonics were considered as significant until the mean Z-score across all conditions was no longer above 1.64 ($P < 0.05$, one-tailed, for testing signal above noise) for 2 consecutive harmonics. Based on this criterion, the oddball response was quantified as the sum of the oddball harmonics until the 14th harmonic (i.e. $14F/5 = 16.46$ Hz), excluding harmonics corresponding to the base rate frequency $F = 5.88$ Hz and its second harmonic ($2F = 11.76$ Hz). The response at the base frequency rate, which reflects the synchronization of the visual system to the stimulation and represents the overall response to the alternation of the gray background and the facial images, was quantified as the summed response of the base rate and its following 2 harmonics: $2F = 11.76$ Hz and $3F = 17.64$ Hz.

Since the response at a particular EEG frequency reflects the overall noise level and the signal unique to the stimulus presentation, 2 measures to describe the response—SNR and baseline-corrected amplitudes—were used. SNR is expressed as the amplitude value divided by the average amplitude of the 20 surrounding frequency bins (10 on each side, excluding the immediately neighboring bin and the 2 most extreme values, e.g. Liu-Shuang et al. 2014; Dzhelyova and Rossion 2014a). SNR spectra were used for data visualization, since the harmonic responses at high frequency ranges may be of small amplitude but with a high SNR. Combination of oddball harmonics (i.e. $F/5 = 1.18$ Hz, $2F/5 = 2.35$ Hz, etc.) was made by first applying a baseline-correction to the amplitude by subtracting the average noise level of the surrounding 20 bins and then summing the baseline-corrected amplitudes for the significant harmonics of the oddball frequency. This procedure has the advantage that the response is expressed in amplitude (μV) in order to combine (i.e. sum) the oddball harmonics for a quantification of the overall oddball response (Dzhelyova and Rossion 2014a). Grand-averages of the SNR and baseline-corrected amplitudes were computed for each condition and electrode separately.

Based on several previous studies using a similar paradigm (Liu-Shuang et al. 2014; Dzhelyova and Rossion 2014a, 2014b) and on inspection of the topographical maps, analysis of the base rate frequency (5.88 Hz and its harmonics), although it was not the main goal of the present study, focused on 3 regions of interest: medial occipital (around Oz), and lateral occipital (around PO7 and PO8 for left and right hemisphere, respectively). Since this is the first study with a FPVS approach on facial expression discrimination, oddball responses, indexing the detection of a change of expression, were first considered over the whole scalp based on grand-averaged data for each expression change in upright orientation.

Brain topographical analysis. Visual inspection pointed to scalp topographical differences among the 3 facial expression changes. The response to a change from neutral to happy expression was characterized by a more dorsal distribution over posterior electrode sites than the responses to a change from neutral to fearful or to disgusted faces. The change from neutral to disgusted faces was characterized with a more anterior temporal scalp topography than the change to fearful faces. To quantitatively evaluate these topographical differences, individual baseline-corrected FFT spectrum data for each facial expression in upright and inverted orientation was normalized. For each participant, the baseline-corrected spectrum for each condition was first scaled by dividing the value at each electrode by the scalp-wide root-mean-square value (i.e. the square root of the sum of squares for all 128 electrodes) (McCarthy and Wood 1985). These normalized amplitudes were then summed for the significant harmonics and evaluated with repeated measures ANOVA with *Facial Expression* (Fear, Disgust, Happiness) and *Electrode* separately for 2 scalp halves: anterior/frontal and posterior. The scalp was split through the midline and the 66 anterior/frontal electrodes formed the anterior/frontal half while the remaining 62 electrodes formed the posterior half. Importantly, an interaction between *Facial Expression* and *Electrode* would indicate differences between the topographical distributions, thus hinting at partly distinct neural generators of the observed scalp response.

In addition, a decoding approach was used to evaluate if potential differences in the spatial organization of the neural sources generating scalp responses across the different emotions were present. Decoding was performed in each subject and classification performance was averaged across subjects. An average of 3 sequences was used as a training set while the remaining last sequence was used as a test set for the classifier. All possible combinations across the sequences were evaluated, so that the classifier performance per condition for each participant can range between 25% and 100% accuracy. To avoid general amplitude differences across electrodes driving decoding performance, the classification was performed on the normalized baseline-corrected amplitudes. We then use a winner-take-all maximum correlation classifier, which predicts the category of the test sequence based on the highest correlation between the topography of the test sequence and the 3 training topographies (fear, disgust, and happiness).

Time-domain analysis. Time-domain analysis was performed to visualize the shape of the periodic changes time-locked to the oddball stimulus, and estimate the speed and time course of facial expression changes. Preprocessed and re-referenced data were low pass FFT filtered at 30 Hz with filter width of 1 Hz. A FFT notch filter with 0.1 Hz width selectively removed the dominating base frequency, 5.88 Hz, and its harmonics (i.e. 11.76 Hz, etc., see Dzhelyova and Rossion 2014a). The first and last 2 s of the sequence corresponding to the fade in and fade out were excluded. Overlapping stimulus locked epochs were segmented, lasting for an overall duration of 2000 ms (12 cycles of the base rate locked to an oddball presentation). For each sequence, 94 epochs were available per repetition for each condition (94 oddball images × 850 ms per cycle = 79 900 ms). Epochs with channels amplitude above ± 100 μV were rejected. On average, 298 epochs were available with no significant differences across conditions (*Orientation*, $F(1, 17) = 0.59$, $P = 0.81$; *Facial Expression*, $F(2, 34) = 1.13$, $P = 0.34$), or the interaction between *Orientation* and *Facial Expression*, $F(2, 34) = 1.70$, $P = 0.20$. These epochs were averaged for each participant and baseline corrected by subtracting the signal within the 170 ms pre-stimulus presentation, corresponding roughly to 1 cycle of the base rate. These baseline-corrected epochs were then grand-averaged for each condition separately.

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Results

Behavioral Data of the Change of Fixation Color Task

A repeated measures ANOVA with *Orientation* (Upright; Inverted) and *Facial Expression* (Fear; Disgust; Happiness) as within-subject variables indicated no differences in task performance between upright and inverted faces (accuracy: $F(1, 17) = 0.03$, $P = 0.85$; RT: $F(1, 17) = 1.57$, $P = 0.22$) as well as between the different facial expressions (accuracy: $F(2, 34) = 1.44$, $P = 0.25$; RT: $F(2, 34) = 2.65$, $P = 0.09$). The interaction between *Orientation* and *Facial Expression* did not reach significance for accuracy, $F(2, 34) = 0.95$, $P = 0.40$ or correct RTs, $F(2, 34) = 3.02$, $P = 0.06$.

Behavioral Data of the Explicit Facial Expression Change Detection

Data from one of the 18 participants for the behavioral facial expression discrimination task were not collected. The *Facial Expression* of the faces had no effect on accuracy rates, which were high for all conditions ($F(2, 32) = 0.88$, $P = 0.42$, Fearful faces: $M = 0.92$, $SEM = 0.02$; Disgusted faces: $M = 0.94$, $SEM = 0.02$; Happy faces: $M = 0.94$, $SEM = 0.02$), indicating that participants were able to explicitly detect the changes of facial expression at this fast rate if requested to. There were small but significant differences in correct response times, $F(2, 32) = 4.45$, $P = 0.02$, $\eta_p^2 = 0.22$: Happy faces ($M = 500$ ms, $SEM = 11.5$) were detected slightly faster than fearful faces ($M = 521$ ms, $SEM = 13.2$, $P = 0.04$ with a Bonferroni correction for multiple comparisons) but did not differ from disgusted faces ($M = 512$, $SEM = 12.1$, $P = 0.35$). The speed of detection of the latter expressions did not differ significantly ($P = 0.51$). Since the number of false alarms (neutral faces indicated as expressive) was very small (on average across participants $M \leq 1$, range 0–4) these responses were not further analyzed.

EEG Data: Frequency Analysis

Base Frequency: General Visual Stimulation

The base frequency rate response merely reflects the contrast between the background and the face stimuli. It is a mixture of low-level and high-level processes (see e.g. Dzhelyova and Rossion 2014b). It was not the main focus of the study and this response was not expected to differ between facial expressions. Similarly to our previous experiments with this paradigm (e.g. Liu-Shuang et al. 2014, Dzhelyova and Rossion 2014a), the 5.88 Hz response was characterized by a medial occipital topography peaking at Oz for the response at the fundamental frequency rate ($F = 5.88$ Hz: 1.77 µV; $SNR = 16.66$) and the harmonics ($2F = 11.76$ Hz: 1.12 µV; $SNR = 15.07$; $3F = 17.64$ Hz: 0.54 µV; $SNR = 11.12$). For upright faces, at the fundamental frequency (5.88 Hz), the activity spread towards lateral occipital sites, particularly over the right hemisphere (Fig. 2), also in line with our previous observations (Alonso-Prieto et al. 2013; Liu-Shuang et al. 2014, Dzhelyova and Rossion 2014a). To explore the effects of *Orientation* (Inverted, Upright) and *Facial Expression* (Fear, Disgust, Happiness), regions of interest over the 3 electrodes showing the largest response were defined: medial occipital (mO: POOz, Oz, OIz); right occipito-temporal (rOT: PO8, PO10, P10); and left occipito-temporal (lOT: PO7, PO9, P9) regions. The baseline-corrected amplitudes summed for the 3 harmonics of the base rate were compared. The repeated measures ANOVA with *ROI* (mO, rOT, lOT), *Orientation* (Inverted, Upright), and *Facial Expression* (Fear, Disgust, Happiness) revealed a main effect of *ROI*, $F(2, 34) = 17.36$, $P < 0.0001$, $\eta_p^2 = 0.51$, and *Orientation*, $F(1, 17) = 9.89$, $P = 0.006$, $\eta_p^2 = 0.37$ (with an average of 29% increase in response to upright as compared to inverted faces). These 2 main effects were qualified by a significant interaction between *Orientation* and *ROI*, $F(2, 34) = 7.22$, $P = 0.002$, $\eta_p^2 = 0.30$. Investigating each ROI (lOT, mO, rOT) separately revealed that the significantly increased response for upright compared to inverted faces was present for the lOT (31% increase), $F(1, 17) = 7.07$, $P = 0.016$, $\eta_p^2 = 0.29$ and rOT (55% increase), $F(1, 17) = 20.29$, $P < 0.0001$, $\eta_p^2 = 0.54$ but not for the mO region (2% increase), $F(1, 17) = 0.13$, $P = 0.72$. No other main effects or interactions reached significance ($Ps > 0.15$).

In summary, we observed larger responses to upright than inverted faces at the base stimulation rate, this difference being non-significant over medial occipital sites where responses to low-level stimuli are typically recorded. However, there were significant differences over left and right lateral occipital/occipito-temporal electrode sites typical of high-level visual responses (Liu-Shuang et al. 2014; Rossion 2014).

Oddball Frequency: Discrimination of Expression

A clear oddball response can be seen in the EEG spectrum (Fig. 3), at 1.18 Hz and harmonics, with the highest SNR observed on the third and fourth harmonics (i.e. 3.53; 4.70 Hz) for all conditions, as reported previously for changes of face identity (Liu-Shuang et al. 2014; Dzhelyova and Rossion 2014a). Here this response reflects the detection of the brief changes of facial expression. The response was much larger for upright compared to inverted faces over occipito-temporal sites (Fig. 3), to the point where discrimination responses were barely visible when faces were presented upside-down. The magnitude of the inversion effect ((upright-inverted)/inverted) averaged across emotions and the 2 occipito-temporal ROIs reached 140% and 107% for the right hemisphere and left hemisphere, respectively, indicating that face inversion had a stronger impact on the perception of expression change (i.e. oddball rate) than the simple presentation of facial stimuli (i.e. base rate).

Response over the whole scalp. The grand-averaged summed baseline-corrected amplitudes for upright faces, pooled over all channels, revealed the largest oddball response for changes from neutral to disgusted faces (0.55 µV ± 0.03, $z = 11.50$), followed by the response to happy faces (0.46 µV ± 0.03, $z = 11.13$) and to fearful faces (0.43 µV ± 0.02, $z = 10.94$). To ensure that the presence of oddball responses in the grand-averaged EEG spectra were not driven by only few participants in the sample, individual participants' response was averaged across all channels, and summed for the oddball harmonics (changes to Fear: range 0.02–1.0 µV; changes to Disgust: range 0.12–1.1 µV; changes to Happiness: range 0.14–0.93 µV). This response was then compared with a one-sample t-test against 0 (i.e. noise level), showing a significant response for all 3 facial expressions at upright orientation ($Ps < 0.0001$).

A repeated measures ANOVA on the response across the whole scalp with *Orientation* (Upright, Inverted) and *Facial Expression* (Fear, Disgust, Happiness) as within-subject factors revealed a main effect of both *Facial Expression*, $F(2, 34) = 3.31$, $P = 0.049$, $\eta_p^2 = 0.16$ and *Orientation*, $F(1, 17) = 30.89$, $P < 0.0001$, $\eta_p^2 = 0.65$. The interaction between *Orientation* and *Facial Expression* was also significant, $F(2, 34) = 5.27$, $P = 0.01$, $\eta_p^2 = 0.24$, due to the smaller difference between upright and inverted faces for fearful, $t(17) = 2.43$, $P = 0.026$, compared to disgusted, $t(17) = 4.26$, $P = 0.001$, and happy faces, $t(17) = 6.50$, $P < 0.0001$.

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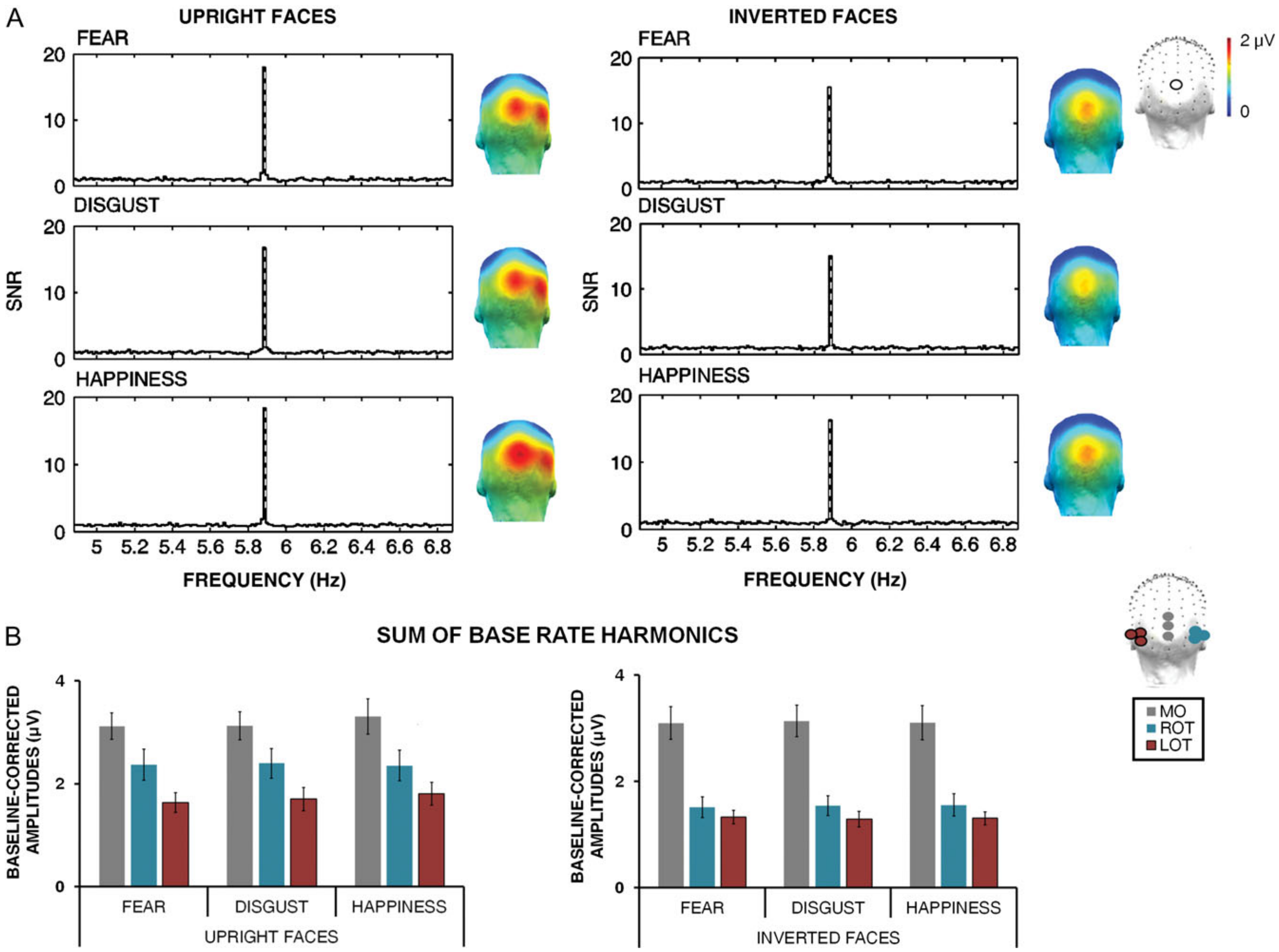

Figure 2. Base rate response. (*A*) Grand-averaged SNR spectra (displayed from 4.88 to 6.88 Hz, centered on 5.88 Hz) over channel Oz for the different facial expressions (fear, disgust, and happiness) presented at upright (left panels) and inverted (right panels) orientations. Topographical maps are plotted for the response at 5.88 Hz, showing neural activity over lateral occipital regions for upright faces only. (*B*) The summed baseline-corrected harmonics of the base rate (5.88 Hz; 11.76 Hz; 17.64 Hz) for the MO (medial occipital); right OT (occipito-temporal); left OT (occipito-temporal) regions. Error bars are standard errors of the mean. A response above 0 reflects signal > noise. Note that the response over the MO and right OT regions for the base rate 5.88 Hz is larger for upright than inverted faces (*A*). Yet, when all harmonics are considered, this difference disappears over the MO region (*B*). The remaining difference over the right and left OT regions is driven by the response at the first harmonic (5.88 Hz).

The main effect of *Facial Expression* did not reach significance for upright faces, $F(2, 34) = 2.93$, $P = 0.067$. However, despite the small oddball response for inverted faces, there was an effect of *Facial Expression* for these stimuli, $F(2, 34) = 7.11$, $P = 0.003$, $\eta_p^2 = 0.30$. The effect of *Facial Expression* for inverted faces was due to higher amplitudes for changes to fearful faces, particularly when compared to the response to changes to happy faces ($P = 0.001$ with a Bonferonni correction for multiple comparisons).

ROI analysis. To further explore the differences between the discrimination of the 3 facial expressions, 2 regions of interest (ROIs, dorsal and ventral) within the right occipito-temporal sites were defined for further analysis. Each ROI comprised 3 electrodes with the highest baseline-corrected amplitudes, excluding the electrodes that overlapped across the 2 regions. The first ROI (electrodes PO10, PO12, P10) was more ventral, where the peak of the response to discrimination of fearful and disgusted facial expressions was observed. The other ROI was more dorsal (electrodes POO6, PO8, PPO6), encompassing the peak of the discrimination between neutral and happy facial expressions (Fig. 3). In order to investigate hemispheric differences, the corresponding electrodes in the left hemisphere were included in the analysis.

The amplitudes were analyzed with a repeated measures ANOVA with within-subject factors *ROI* (Ventral, Dorsal), *Hemisphere* (Left, Right), Orientation (Upright, Inverted) and *Expression* (Fear, Disgust, Happiness). A main effect of *Orientation*, $F(1, 17) = 31.20$, $P < 0.0001$, $\eta_p^2 = 0.65$, confirmed the observation that the oddball response to upright faces was larger than the response to inverted faces. The response to changes of expressions was larger over the right ($M = 0.95$; $SEM = 0.13$) than the left ($M = 0.79$; $SEM = 0.08$) hemisphere, although this difference did not reach significance, $F(1,17) = 3.16$, $P = 0.095$, $\eta_p^2 = 0.15$. A main effect of *ROI*, $F(1, 17) = 9.51$, $P = 0.007$, $\eta_p^2 = 0.36$, indicated that the response over the ventral region ($M = 0.97$, $SEM = 0.12$) was larger than the response over the dorsal region ($M = 0.78$, $SEM = 0.12$). A main effect of *Expression*, $F(2, 34) = 3.88$, $P = 0.030$, $\eta_p^2 = 0.19$, pointed to differences among the 3 expressions. Importantly, however, the latter 2 main effects were qualified with a significant interaction between *Expression* and *ROI*, $F(2, 34) = 3.86$, $P = 0.031$, $\eta_p^2 = 0.19$. Similarly, the interactions between *ROI* and

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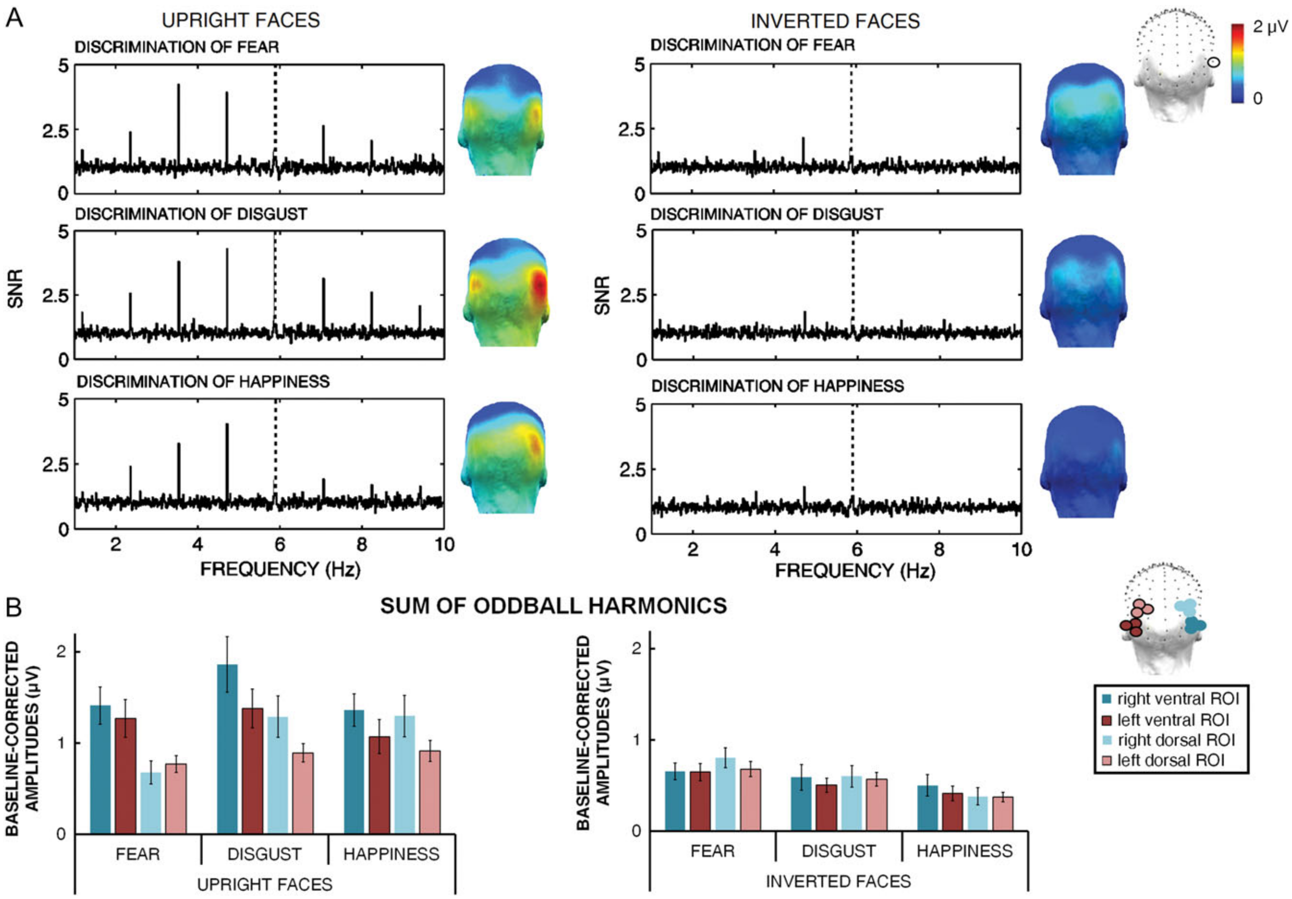

Figure 3. Oddball response to facial expression changes. (*A*) Grand-averaged spectra for the oddball response (displayed from 1 to 10 Hz) over the occipito-temporal electrode P10 in the right hemisphere, for upright and inverted faces, reflecting the changes of facial expressions (i.e. from neutral to either fear, disgust, or happiness). Note that the fifth harmonic (marked with a dashed line) corresponds to the base rate, 5.88 Hz. Topographical maps of the grand-averaged data show the sum of baseline-corrected amplitudes (μV) for the oddball response up to 16.46 Hz for upright and inverted faces. (*B*) Summed baseline-corrected oddball amplitudes (until 16.46 Hz, excluding the base rate harmonics 5.88 Hz, marked with a dashed line, and 11.76 Hz) for the 2 (dorsal and ventral) right and left OT (occipito-temporal) ROIs. Error bars are standard errors of the mean. A response above 0 reflects signal > noise.

Orientation, $F(1, 17) = 26.97$, $P < 0.0001$, $\eta_p^2 = 0.61$, *Orientation* and *Expression*, $F(2, 34) = 6.33$, $P = 0.005$, $\eta_p^2 = 0.27$ and the 3-way interaction among *ROI*, *Orientation* and *Expression*, $F(2, 34) = 10.82$, $P < 0.0001$, $\eta_p^2 = 0.39$ reached significance. All other interactions did not reach significance ($P > 0.05$).

To decompose the significant 3-way interaction among *ROI*, *Orientation* and *Expression*, 2 separate repeated measures ANOVAs for upright and inverted faces were performed. The interaction between *Expression* and *ROI* was significant for both upright faces, $F(2, 34) = 9.00$, $P = 0.001$, $\eta_p^2 = 0.35$ and inverted faces, $F(2, 34) = 3.55$, $P = 0.04$ ($P > 0.025$). For upright faces, in the ventral posterior occipital ROI, a facial expression change to disgust led to a larger response than a facial expression change to happiness ($P = 0.047$ with a Bonferroni adjustment for multiple comparisons). In the dorsal region, a facial expression change to happiness and to disgust led to a larger response than a change to fear ($P \leq 0.022$ with a Bonferroni adjustment for multiple comparisons) (Fig. 3). For inverted faces, only in the dorsal region, changes to fearful faces produced a stronger response than changes to happy faces ($P < 0.0001$ with a Bonferroni adjustment for multiple comparisons).

Analysis in individual participants. The response to facial expression changes in upright faces was also evaluated in individual participants. To visualize the overall response for each individual participant, we cropped the FFT spectrum, centered at the oddball response (1.18 Hz and the subsequent harmonics until 11.67 Hz), surrounded by their neighboring bins (each bin corresponded to 0.0125 Hz), representing the noise level. Then, we summed the spectrum including the response and the noise level and applied a baseline-correction by subtracting the average noise level of the surrounding 10 bins excluding the immediately adjacent and the maximal ones. In the absence of a signal at the central bin of interest, the value at this bin has 1 chance out of 21 (i.e. $P < 0.05$) to be the highest in the spectrum. Results of this analysis are displayed in Figure 4. Strikingly, all of the individuals tested in the study showed a clear peak (centered in the middle of the displays) corresponding to the detection of expression change within the left/right temporal-occipital region (channels PO10, PO12, P10 and the corresponding left hemisphere channels for disgusted and fearful faces; channels POO6, PO8, PO10 and the correponding left hemisphere channels for happy faces) for the particular expression, or at a channel in close proximity. When considering the response to expression change from neutral to fearful faces, only one participant (P13) showed the largest response outside of this region, at electrode C3, corresponding to the area over the left side of the vertex.

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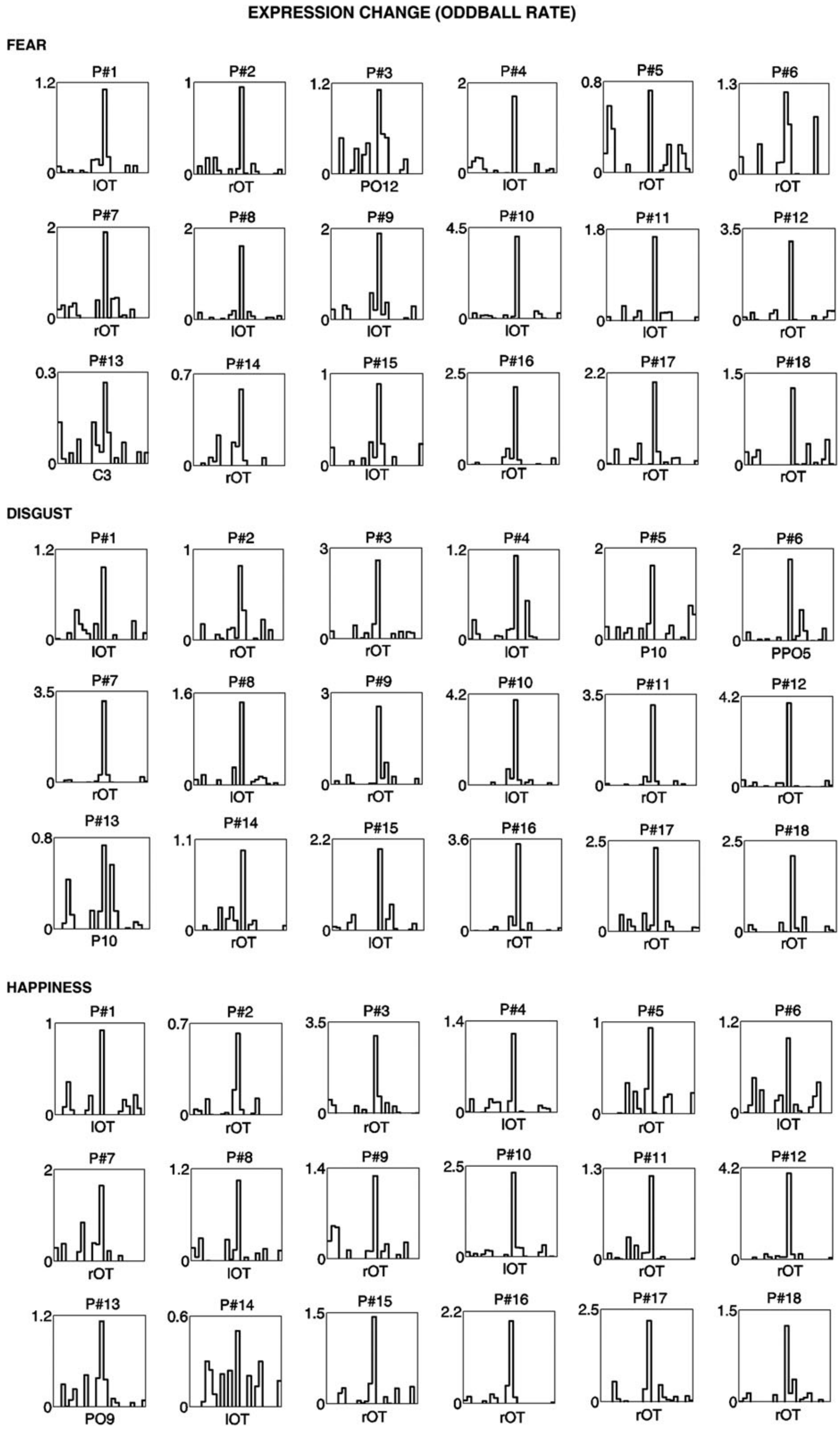

Figure 4. Individual participants' EEG responses to changes of facial expression in the frequency domain. Baseline-corrected amplitudes for the three emotions (fear, disgust and happiness) in the upright orientation over occipito-temporal regions (channels PO10, PO12, P10 and the corresponding left hemisphere channels for the disgusted and fearful faces and channels POO6, PO8, PO10 and the corresponding left hemisphere channels for happy faces). The EEG spectra are centered at the frequency bin corresponding to the response to expression changes (summed oddball responses until 16.52 Hz, excluding frequencies corresponding to the base rate). It is surrounded by 12 neighboring bins, indicating noise levels. Hemispheric dominance is noted underneath the displays. Note: For participant 13 (P13) the response to expression change from neutral to fear is displayed over channel C3 (channel within the area of the vertex, see main text).

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Scalp topography analysis. This analysis was performed to test for spatial differences between the responses to the different kinds of expression changes when presented at upright orientation, separately for the 2 halves (posterior and anterior) of the scalp, split along the midline (see Methods).

For posterior channels, the repeated measures ANOVA with *Facial Expression* (Fear, Disgust, Happiness) and *Electrode* (62 posterior electrodes) revealed a main effect of *Facial Expression*, $F(2, 34) = 5.35$, $P = 0.01$, $\eta_p^2 = 0.24$ and *Electrode*, $F(61, 1037) = 17.40$, $P < 0.0001$, $\eta_p^2 = 0.51$. More importantly, there was a highly significant interaction between *Facial Expression* and *Electrode*, $F(122, 2074) = 2.58$, $P < 0.0001$, $\eta_p^2 = 0.15$, due to differences in scalp topographies between the 3 types of facial expression changes. To follow-up this interaction and explore further the differences between the facial expressions, each topographical distribution corresponding to a facial expression was compared to the topographical distribution of the other 2 expressions separately. All these comparisons were significant (i.e. a significant interaction between *Electrode* and *Facial Expression*: fearful vs. disgusted, $F(61\,1037) = 2.39$, $P < 0.0001$; fearful vs. happy, $F(61, 1037) = 3.14$, $P < 0.0001$, disgusted vs. happy, $F(61, 1037) = 2.11$, $P < 0.0001$).

When evaluating the anterior/frontal half of the electrodes only, the interaction between *Facial Expression* and *Electrode* did not reach significance, $F(130, 2210) = 0.59$, $P > 0.99$, indicating that the topographical differences were mainly driven by variations at posterior sites.

For inverted faces, this interaction between *Facial Expression* and *Electrode* did not reach significance for the anterior/frontal halves, $F(130, 2210) = 0.85$, $P = 0.88$ while the significant interaction over the posterior sites, $F(122, 2074) = 1.328$, $P = 0.011$ was driven only by a significant difference between changes to happiness and changes to fearful faces, $F(61\,1037) = 2.07$, $P < 0.0001$.

The classifier could decode above chance (chance level across participants: 33%) the variations in the topographical organization of the different expressions for upright faces (i.e. classification of all emotions was above chance: mean decoding performance for Fear = 44.44, SD = 31.57, P = 0.052; Disgust = 48.16, SD = 31.47, P = 0.011; Happiness = 50.00, SD = 33.21, P = 0.010), but not for inverted faces (none of the topographies was classified above chance level: Fear = 36.11, SD = 27.41; Disgust = 31.94, SD = 22.36; Happiness = 34.72, SD = 27.30 all Ps > 0.30).

EEG Data: Time Domain

An evoked oscillation at 5.88 Hz was prominent on the averaged EEG data containing the base rate. For upright faces, it was disrupted, or modulated, by responses time-locked to the onset of a change to an expressive face (Fig. 5). On the unfiltered EEG data, these responses were barely visible when faces were inverted. When the base rate signal was selectively filtered out, there were 2 clear differential responses discriminating emotional from neutral upright faces: a negativity peaking shortly after 200 ms, followed by a wider positivity between 300 and 450 ms (Fig. 5).

Summary of Results

In summary, we revealed a clear response to brief changes from a neutral face to an expressive face, as indexed by a robust oddball frequency response in the EEG: the frequency-domain oddball response was present for all individual participants in all conditions for only a few minutes of recording. For all 3 expression changes, this response was distributed over occipito-temporal sites, with a right hemisphere advantage, and was drastically decreased when facial images were presented at an inverted orientation. Differences in the absolute magnitude of the expression change-related response for the different kinds of expressions were observed across the 2 regions within the occipito-temporal sites. These differences were also reflected in a specific topographical signature on the scalp, pointing to differences in the spatial organization and/or the extent to which the populations of neurons coding for the detection of these brief expression changes were activated. A

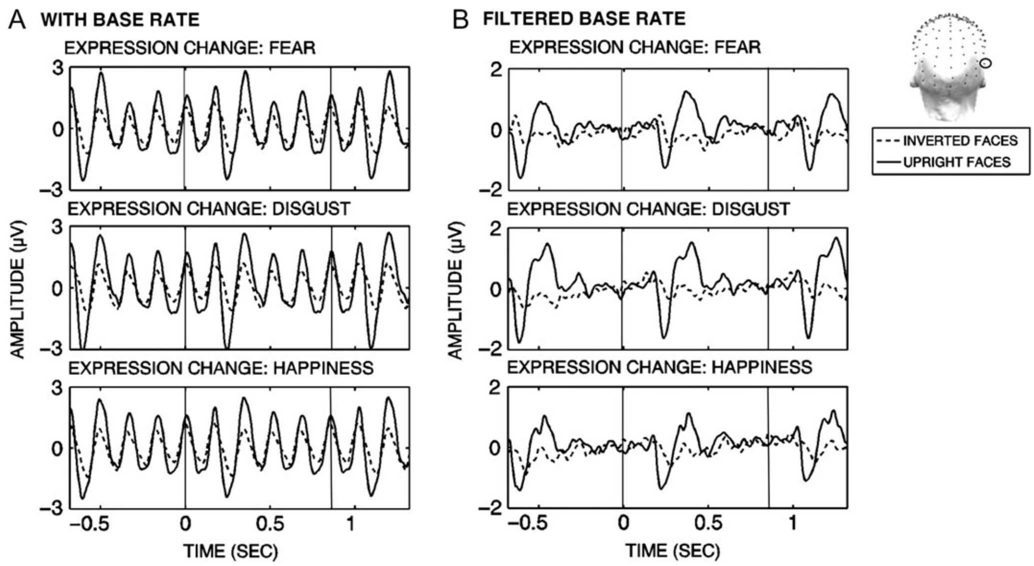

Figure 5. Time-domain data comparing the discrimination response to upright and inverted expressive faces. Data are displayed over occipito-temporal electrode P10 (right hemisphere) for upright (solid line) and inverted (dashed line) faces for all 3 expressions (fear, disgust, happiness) (*A*) with the base rate at 5.88 Hz; (*B*) after selectively filtering out the base rate to reveal the differential components superimposed on this base rate oscillation. Data are displayed for a segment of 2 s time-locked to the presentation of the expression change, marked with a black line at 0, showing 3 presentations of an expression change. A small early positive deflection is followed by 2 main differential components, clearly visible in all 3 conditions.

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time-domain analysis revealed a complex response comprised of several components starting from 200 ms post-expression change, and contributing to the harmonics of the oddball responses in the frequency domain.

Experiment 2

In experiment 1, due to the sinusoidal contrast stimulation, the facial stimuli were fully revealed (i.e. 100% contrast) 85 ms after stimulus onset and were thus hardly visible for the first 25–30 ms, resulting in a delay of the discrimination responses. To strengthen our findings and to explore further these time-domain responses, we performed a second experiment in which we compare a square wave (i.e. abrupt onset) to a sine wave stimulation mode. In addition, we used an even faster base presentation rate of 12 Hz, for 2 reasons. First, a base rate above 10 Hz for face stimulation should evoke reduced activity over occipito-temporal regions, with a maximum at medial occipital sites (Alonso-Prieto et al. 2013), thus spatially separating better the base rate response (i.e. onset of the face against the background) from the oddball rate response (i.e. reflecting expression change). Second, this faster stimulation rate tested whether changes of expression could be detected for even briefer durations of stimulus presentation. By changing the oddball proportion, a ratio of roughly 10% of oddball stimuli, our paradigm is also more comparable to standard vMMN paradigms, in which the oddball proportion rate typically ranges between 10% and 20% (e.g. Astikainen and Hietanen 2009; Stefanics et al. 2012; Astikainen et al. 2013).

Methods

Stimulation

Fifteen participants (5 males, age $M = 23.27$, $SD = 4.22$) who did not take part in experiment 1 took part in this second experiment. The same facial stimuli were used, but only at the upright orientation. They were presented at 12 Hz (SOA 83.33 ms) and the oddball expression changes appeared every ninth stimulus, resulting in an oddball frequency of 1.33 Hz, i.e. roughly 750 ms duration between the presentations of 2 oddballs. The experiment consisted of 24 sequences: 3 Facial Expression (Fear, Disgust, Happiness), displayed at 2 Presentation Mode (Sine wave; Square wave), repeated 4 times with different identities (2 females and 2 males). Similarly to the first experiment, when facial images were presented sinusoidally, they reached full contrast half way through the cycle, approximately 42 ms after image onset (1000/12 Hz)/2, while when presented with a square wave, images reached full contrast (0–100%) within one frame of the screen refresh rate. During both modes of stimulations, images alternated with a gray background, as in experiment 1. Each stimulation sequence started with a fixation cross presented for a variable duration of 2–5 s, followed by a fade in of 4 s, the stimulation sequence of 80 s and a 4 s of stimulus fade out. The rest of the testing protocol was the same as described in experiment 1.

EEG Analysis

Preprocessing

The same frequency-domain analysis as in experiment 1 was performed. Firstly, the continuously recorded data were segmented into sequences of 92 s corresponding to 2 s before the start of the sequence and 2 s after the end of it. A Butterworth bandpass filter at 0.1 Hz–100 Hz (fourth order) was applied. Following this, data were resampled to 250 Hz and, if necessary, noisy or artifact-ridden channels were interpolated by applying a linear interpolation of the 3 artifact-free spatially neighboring channels. All data were re-referenced to a common grand-averaged reference.

Frequency Domain

Pre-processed data were cropped to an integer number of oddball cycles (106–79.52 s). Due to the fast frequency of stimulation, the base response was characterized with a typical medial occipital topography, peaking at Oz and without spreading to occipito-temporal regions (Alonso-Prieto et al. 2013). Therefore only the mO region (POOz, Oz, OIz) was evaluated in the analysis, examining any differences in the response depending on the *Presentation Mode* (Sine wave; Square wave) and *Facial Expression* (Fear; Disgust; Happiness). In order to compare the response of the 2 experiments, the oddball response was evaluated until 16 Hz (1.33 Hz and the subsequent 11 harmonics). Visual evaluation of the topographical distribution of the summed baseline-corrected oddball response suggested that the same ROIs were maximally activated. In the right hemisphere, electrodes PO10, PO12, P10 were included as a ventral occipito-temporal ROI while channels POO6, PO8, and PPO6 were included as a dorsal occipito-temporal ROI. The corresponding channels of the left hemisphere were also evaluated.

Time Domain

Since the analysis focused on the time domain, an additional ICA, as described in the first experiment, was applied to remove blink artifacts for all participants' data. Similarly to the time-domain analysis of the first experiment, a low pass FFT filter at 30 Hz, width of 1 Hz, was applied to the re-referenced segments. A notch FFT filter at 12 Hz with width 0.1 Hz selectively removed the base rate and its second harmonic (24 Hz). Following this, 2 s long overlapping epochs were cropped, locked to the presentation of an oddball stimulus, resulting in 106 epochs per sequence, overall 424 epochs per condition. These notch filtered epochs were averaged per participant and per condition separately, baseline corrected with the mean amplitude of the wave for 83.33 ms before the oddball presentation, corresponding to 1 cycle of the base rate. A t-test comparing when the waveforms were significantly different from 0 ($P < 0.05$, for at least 5 consecutive points, approximately 20 ms) was performed.

Results

Frequency Domain

Base Frequency: General Visual Stimulation

A repeated measures ANOVA with *Facial Expression* (Fear; Disgust; Happiness) and *Presentation Mode* (Sine wave; Square wave) revealed only a main effect of *Presentation Mode*, $F(1, 14) = 20.70$, $P < 0.0001$, $\eta_p^2 = 0.59$, indicating increased amplitudes for the base rate when stimuli were presented through a square wave compared to when the stimuli were sinusoidally presented. The main effect of *Facial Expression* did not reach significance, $F(2, 28) = 1.84$, $P = 0.18$; neither did the interaction between *Facial Expression* and *Presentation Mode*, $F(2, 28) = 0.05$, $P = 0.95$.

Oddball Frequency: Discrimination of expression

Similarly to experiment 1, the baseline-corrected amplitudes were analyzed with a repeated measures ANOVA with

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within-subject factors 2 posterior-occipital *ROI* (Ventral; Dorsal), 2 *Hemisphere* (Left; Right), 2 *Presentation Mode* (Sine wave; Square wave) and 3 *Facial Expression* (Fear; Disgust; Happiness). The response to changes from neutral to expressive faces did not differ across the 2 presentation modes, $F(1, 14) = 0.02$, $P = 0.88$. The main effect of *Facial Expression* was significant, $F(2, 28) = 6.83$, $P = 0.004$, $\eta_p^2 = 0.33$. Yet, similarly to the first experiment, this effect was qualified by a significant interaction between *Facial Expression* and *ROI*, $F(2, 28) = 5.79$, $P = 0.008$, $\eta_p^2 = 0.29$. Investigating separately the ventral and the dorsal posterior-occiptal ROIs revealed that the main effect of *Facial Expression* was significant in both ROIs (Ventral: $F(2, 28) = 4.17$, $P = 0.026$, $\eta_p^2 = 0.23$; Dorsal: $F(2, 28) = 8.37$, $P = 0.001$, $\eta_p^2 = 0.37$). In the ventral region, changes to disgusted faces produced a slightly larger response than changes to fearful faces (NS, $P = 0.058$ with a Bonferroni correction for multiple comparisons) while in the dorsal region, the changes to happiness led to a stronger response than changes to fear ($P = 0.011$, Bonferroni corrected) and a non-significant trend for a stronger response to changes to disgust compared to changes to fear ($P = 0.090$, Fig. 6).

In addition to the significant interaction between *Facial Expression* and *ROI*, the interaction between *Hemisphere* and *Facial Expression*, $F(2, 28) = 6.26$, $P = 0.006$, $\eta_p^2 = 0.31$ and the 3-way interaction among *Hemisphere*, *Presentation Mode*, and *Facial Expression*, $F(2, 28) = 3.39$, $P = 0.048$; $\eta_p^2 = 0.20$, were also significant. A follow-up analysis revealed that the interaction between *Hemisphere* and *Facial Expression* was present for both the square wave mode, $F(2, 28) = 5.34$, $P = 0.011$, $\eta_p^2 = 0.27$ and the sine wave mode, $F(2, 28) = 6.52$, $P = 0.005$, $\eta_p^2 = 0.32$ due to smaller hemispheric differences for fearful expressions.

None of the other main effects or interactions reached significance in the ANOVA with factors *ROI* (Ventral; Dorsal), *Hemisphere* (Left; Right), *Presentation Mode* (Sine wave; Square wave), and *Facial Expression* (Fear; Disgust; Happiness).

To summarize, the frequency-domain analysis of the second experiment largely replicates the robustness of the facial expression discrimination response observed over occipito-temporal sites. It shows that extremely brief (i.e. <83.3 ms) changes of expression (neutral to happy, fearful or disgusted) can be reliably picked up by the human brain. Overall, although there were slight differences in terms of topographical maps for the different facial expression changes with

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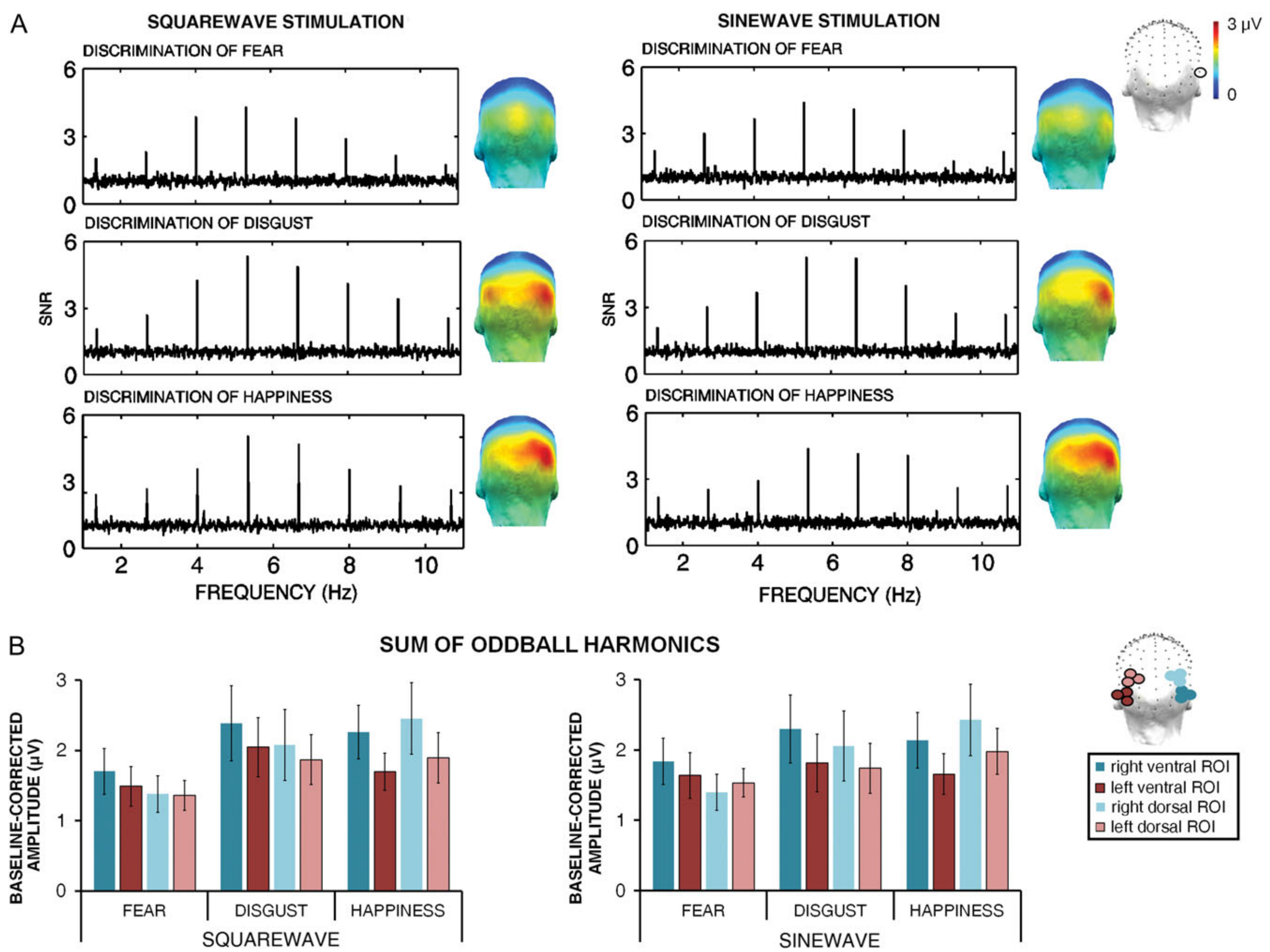

Figure 6. Oddball response to facial expression changes when images are presented through a sine wave or square wave stimulation mode. (*A*) Grand-averaged spectra for the oddball response (displayed from 1 to 10 Hz) over occipito-temporal electrode P10 in the right hemisphere for changes of facial expressions (fear, disgust, happiness) in upright faces presented with a square mode of stimulation (left panel) or sine wave of stimulation (right panel). Topographical maps of the grand-averaged data show the sum of baseline-corrected amplitudes (µV) for the oddball response up to 16 Hz. (*B*) Summed baseline-corrected oddball amplitudes (until 16 Hz, excluding the base rate harmonics 12 Hz for the right and left 2 (ventral and dorsal) OT (occipito-temporal) ROIs. Error bars are standard errors of the mean. A response above 0 reflects signal > noise.

experiment 1, these results show a high degree of consistency across stimulation and oddball rates, as well as presentation mode. Taken together, the findings from experiments 1 and 2 indicate that within the dorsal occipito-temporal region, brief changes from neutral to happy expressions led to the largest response while within the ventral occipito-temporal region changes to disgust produced the largest response. Changes to disgust were recorded both over the dorsal and ventral ROIs while changes to fearful faces were observed mainly over the ventral occipito-temporal region.

Time Domain

Three clear differential responses were evoked by the brief change of facial expression from neutral faces (Fig. 7A). When images were presented with a square wave contrast modulation, the first positive differential response peaked at 110–120 ms post-stimulus depending on condition and channel. This response was localized over more dorsolateral occipital, or parietal electrodes (Fig. 7B). The second response, the negativity clearly identified in experiment 1, significantly differed from 0 for the time period of 160–200 ms post-expression change onset, and peaked at about 170 ms. It was distributed bilaterally over occipito-temporal sites. The last response was also a positivity broadly distributed over medial, lateral, and anterior occipito-temporal sites bilaterally, starting at about 210–230 ms and lasting until 310 ms. The exact same responses were found when the images were presented with a sine wave contrast modulation, yet they were delayed by approximately 20 ms. Thus, the delay due to the sinusoidal presentation was of 20 ms on average, corresponding to roughly ¼ of the sine cycle. These observations indicate that brief changes of expression isolated with this FPVS paradigm elicit a rich tri-phasic response from about 100 ms to 310 ms.

Discussion

Here we provide original evidence for the capacity of the human brain to detect brief (i.e. one fixation) changes from

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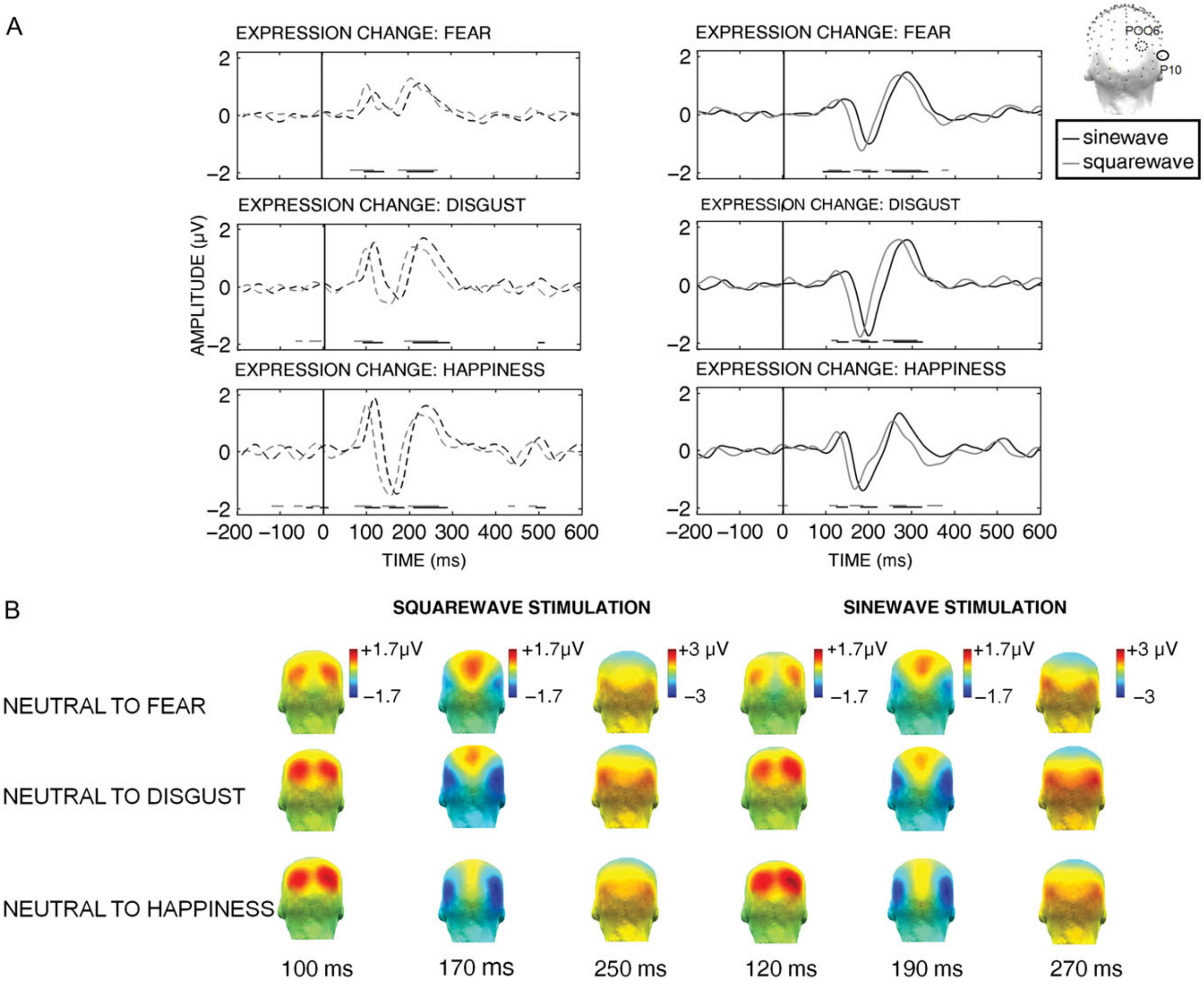

Figure 7. Time-domain data comparing the discrimination response to expressive faces presented through sine wave or square wave stimulation mode. (A) Time-domain data with selectively filtered out 12 Hz base rate for channels POO6 (left panels) and P10 (right panels). Components in response to changes from a neutral face to an emotional face presented as a square wave (gray line) or sinusoidally (black line). Significant time periods at which each of the waveform differs significantly ($P < 0.05$ for at least 5 consecutive points, approximately 20 ms) from 0 are marked in gray (square presentation) and black (sine presentation) horizontal bars. (B) 3D maps represent the topographical distribution of the components discriminating expressive from neutral faces.

neutral to backward- and forward-masked expressive faces. This evidence is shown behaviorally in an explicit discrimination task and, most importantly, in the form of a robust (i.e. high SNR) electrophysiological response obtained without an explicit task. The detection of brief changes of facial expression was identified objectively at the specific frequency rate of the expression change in the EEG (i.e. *n*1.18 Hz) and was significant in every individual participant, following only a few minutes of stimulation. This response was distributed over the occipito-temporal cortex, with a larger response over the right than the left hemisphere, and was substantially reduced when faces were presented upside-down. Despite similar topographical maps, each of the expression changes was associated with a specific reliable topographical distribution, hinting at partially different neuronal generators. In addition, the complementary time-domain analysis revealed a rapid onset (i.e. around 100 ms) yet prolonged response (i.e. up to 310 ms) following the discrimination of the expressive from neutral faces.

A Robust Marker of Brief Expression Changes

Here faces were presented very briefly, i.e. with a 170 ms SOA in experiment 1 and 83.33 ms in experiment 2. Each face appeared in a continuous train of stimulation so that each face stimulus masked the previous one in the sequence. Despite this fast rate, participants were able to explicitly detect the changes of expression accurately and rapidly. In line with previous studies (e.g. Palermo and Coltheart 2004; Calvo and Lundqvist 2008; Bombari et al. 2013), the detection of happy faces was the quickest, possibly due to larger perceptual difference between neutral and positive compared to neutral and negative (e.g. fearful) expressions (Leppänen and Hietanen 2004, 2007).

More notably, however, without explicit processing, brief changes of facial expression elicited a highly significant neural response in the EEG spectrum. This response was virtually identical in the second EEG experiment, when faces were presented with an even shorter SOA (i.e. 83.33 ms). At such high stimulation rates, the response reflects the detection of facial expression changes at a single glance. This is important because there is wide evidence that eye movement patterns differ between neutral and expressive faces or between different facial expressions (Eisenbarth and Alpers 2011; Scheller et al. 2012; Bombari et al. 2013). Thus, while in standard EEG studies, such differential eye movements patterns may contribute to the recruitment of different neural structures, as well as differences observed in EEG for different facial expressions beyond 150–200 ms following stimulus onset, they cannot influence the results obtained here.

Also importantly, the neural marker of a brief facial expression change could be identified objectively in our study: it occurred at a specific EEG frequency pre-determined by the experimenter, i.e. 1.18 Hz in the main experiment 1. The distribution of this EEG response over multiple harmonics (e.g. 2.35 Hz, etc.) merely reflects the complexity of this response in the time domain: at sensitive channels, it is made of multiple components of variable latency, amplitude and width, rather than a simple smooth repetitive oscillation at 1.18 Hz (which would give a single peak at 1.18 Hz in the EEG spectrum, Norcia et al. 2015). This objective identification of the response of interest is a considerable advantage of FPVS, allowing the quantification of this response in a group of subjects and every individual, and making fair comparisons across conditions.

This brief expression change detection signal is extremely robust, and is evidenced significantly in each individual subject tested in the experiment in less than 6 min (i.e. 4 repetitions of 80 s sequences) of visual stimulation at a fast rate of 6 Hz. This sensitivity is much higher than in previous studies investigating differences in facial expression processing using EEG. These studies, even when they are methodologically sound, have often led to highly discrepant results probably due to the lack of objectivity and sensitivity of the approach used. Of particular interest is the comparison between our approach and the non-periodic oddball paradigms, targeting the vMMN component. With the latter approach, numerous trials (e.g. more than 1000; e.g. Astikainen and Hietanen 2009; Stefanics et al. 2012; Astikainen et al. 2013) need to be recorded in order to obtain a clear vMMN response to facial expressions. In addition, due to a relatively low SNR and the focus on different components, vMMN response to changes of expressions cannot be evaluated objectively and quantified at the level of individual participants. These aspects are particularly important since the vMMN is considered as a marker for assessing populations with deficits in processing social cues such as individuals with autism or schizophrenia (e.g. Garrido et al. 2009; Gayle et al. 2012; Maekawa et al. 2012; Cléry et al. 2013). The robustness and sensitivity of the response obtained here to changes of facial expressions suggest that our FPVS paradigm may provide an alternative biomarker for assessing clinical populations' sensitivity to the decoding of facial expression changes.

In this context, it is also important to note that the recorded neural response to brief changes of facial expression largely reflects high-level processes. First of all, it was obtained despite substantial changes of stimulus size at every cycle, so that the changes of expression could not be captured by simple local (i.e. pixelwise) changes of the stimuli (Dzhelyova and Rossion 2014b). Second, a substantially reduced response to changes of expression was found for inverted faces (i.e. more than 120% of signal). This effect cannot be accounted by the inversion effect observed at the base rate frequency (5.88 Hz): the base rate response over the medial occipital site, reflecting a mixture of low- and high-level processes, did not differ significantly between upright and inverted faces. Additionally, the inversion effect over lateral occipital sites for the base rate was much weaker (30–50%) than the significant inversion effect found for the oddball frequency (~120%). Since the performance of the orthogonal task did not differ between upright and inverted faces, it is also unlikely that the increased response to upright faces can be explained by differences in attention or task difficulty. Deficits in recognizing facial expressions in inverted faces have been reported in behavioral studies, but they are often relatively weak (e.g. 10–16%, Prkachin 2003; Calvo and Nummenmaa 2008; Derntl et al. 2009; Bombari et al. 2013). However, in such studies, often stimuli are not masked and are presented until a response is given (e.g. Calvo and Nummenmaa 2008; Bombari et al. 2013), allowing exploration of the face and detection of local differences between neutral and expressive faces even when they are presented upside-down. Moreover, a drop of performance of a few percents in a behavioral task could be due to ceiling/floor effects, and can vary substantially with various tasks. In behavioral studies, inversion seems to affect less, or even to have no effect on, the perception of happy expressions (e.g. Prkachin 2003; Calvo and Nummenmaa 2008; Derntl et al. 2009; Bombari et al. 2013). Here, the inversion effect observed was of comparable size for all facial expressions, although the smallest inversion effect was found for fearful faces. This could be due to face inversion

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primarily affecting the processing of the whole face configuration rather than local face parts (Rossion 2008 for review): since the diagnostic information for recognition of the fearful expression (Smith et al. 2005) is close to the point where participants had to fixate the face (i.e. slightly below the eyes, following Peterson and Eckstein 2012), it would be less affected by inversion.

Finally, it is important to note that our robust results of facial expression change detection were obtained with a particular set of (validated) stimuli displaying prototypical, high intensity facial expression. Therefore, it will be important to generalize these findings with other stimulus sets in the future, test whether they hold for facial expressions found in different human populations (see Jack et al 2012) and across development (e.g. Rodger et al 2015). Moreover, due to the limited number (8 identities) and the nature of these facial stimuli, we acknowledge that the study cannot disentangle the different dimensions contributing to the change of facial expressions, such as arousal and/or valence of the facial images. In addition, given that we were able to find robust results even at a very fast rate of 12 Hz, it is desirable to address the question of the range of presentation rates that are suitable for detecting facial expression changes. Given the high sensitivity of the FPVS oddball paradigm, these issues could be relatively easily addressed in future studies.

Different Changes of Facial Expression Elicit Distinct Spatial Maps

Overall, the response to detecting facial expression changes had a lateral occipito-temporal distribution, with a right hemispheric dominance (Fig. 3). This occipito-temporal distribution is characteristic of high-level visual processes in FPVS, with a right hemisphere specialization for coding the face as a category (i.e. vs. objects; Rossion, et al. 2015) as well as facial identity (e.g. Rossion and Boremanse 2011; Liu-Shuang et al. 2014, Dzhelyova and Rossion 2014b). In general, the coding of facial expressions preferentially engages the right hemisphere, as evidenced by lesion studies and neuroimaging (e.g. Etcoff 1984; Borod et al. 1998; Sato et al. 2004; Tsuchiya et al. 2008; Harris et al. 2012). Yet, when controlling for injury onset, Abbott et al 2014 reported that lesions within both the left and the right hemisphere impaired discrimination of facial expressions. Alternatively, gender of the participants might also play a role in the lateralization of the response (e.g. Wager et al. 2003; Bourne 2005), leading to the less specific lateralization of the discrimination response to changes of facial expressions.

Dynamic information, such as emotional expression, gaze direction, and head orientation is thought to depend relatively more on the lateral and superior regions in the superior temporal sulcus (STS) and gyrus (Allison et al. 2000; Puce and Perrett 2003), while static aspects of a face, such as its gender and identity, are encoded primarily in the ventral occipito-temporal regions (Haxby et al. 2000; Ishai 2008). Complementary to these findings, fMRI studies employing alternations of facial images depicting change in gaze direction or mouth movements strongly activate the STS (Puce et al. 1998, 2003). Thus, the quick transition from neutral to expressive face in the present study, implying dynamic facial expression, could possibly result in activation within this region, leading to the observed occipito-temporal topography. On the other hand, a study with direct intracranial recordings of the human brain during both static and dynamic changes of facial expression from neutral to fear or happy reported a much larger involvement of the ventral than the lateral temporal cortex (Tsuchiya et al. 2008; Kawasaki et al. 2012). Although we can only speculate about the exact neural sources of the EEG responses obtained on the scalp, the scalp topography observed following brief changes of facial expressions is compatible both with sources in the ventral occipito-temporal cortex, such as the fusiform gyrus, and in the lateral temporal cortex, including the STS.

Yet, despite similar maps over the occipito-temporal region, each of the expression changes had its own spatial signature on the scalp, hinting at least at partially separated neural population (for upright faces). Notably the spatial differences between the approach-related expression (happiness), stronger dorsal than ventral occipito-temporal distribution, and the avoidance-related expressions (fear and disgust), stronger ventral than dorsal occipito-temporal distribution, were clearer compared to the difference between the 2 avoidance-related expressions. This distinction could possibly result from a stronger spatial division between the regions processing avoidance- and approach-related expressions. In order to fully address this question, another approach-related expression (e.g. anger) could be examined in future studies. Alternatively, the spatial similarities between processing of changes to disgusted and fearful faces could be due to their perceptual similarities as behaviorally these expressions are often confused (e.g. Palermo and Coltheart 2004; Smith et al. 2005). Nevertheless, to our knowledge, our study provides the first evidence of reliable decoding (i.e. discrimination) of different facial expressions on the scalp, a result owing to the high SNR of the technique and the consistency of the response across individual participants in terms of spatial localization. One potential caveat is that the topographical maps were slightly different between experiments 1 and 2 (Figs. 3 and 6), even though the change to happy expression was associated with the more dorsal scalp topography in both experiments. While these differences between experiments could well be due to interindividual differences in the neural basis of facial expression, they are more likely to be due to the different base frequency rates used in the 2 studies (5.88 and 12 Hz). As mentioned above, future studies testing various frequency rates systematically should be able to clarify the range of presentation rates that are suitable for processing facial expression changes and how that factor affects quantitative and qualitative differences between different kinds of facial expressions.

Recent fMRI studies suggest that the 6 basic expressions could be decoded from activation within the pSTS (Said et al. 2010) and the middle temporal gyrus (Saarimäki et al. 2016). Complementary to these findings, happy and fearful faces were well decoded from the ventral temporal cortex in an intracranial EEG study (Tsuchiya et al. 2008). In line with these observations, the results of the topographical analysis here suggests successful decoding of facial expressions over the occipito-temporal region on the scalp, and complement findings hinting at different neuronal populations involved in the processing of specific expression changes.

Temporal Discrimination Responses for Changes of Expression

Our time-domain analysis revealed at least 3 clear time-domain responses discriminating expressive from neutral faces, for all changes of expression: an early brief and small positivity (100–130 ms), followed by 2 large responses: a negativity (150–210 ms) and a later positivity (210–310 ms). The response was initially focused over posterior dorsal sites, then it

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became more ventral over the occipito-temporal cortex for the latter 2 responses. This pattern was observed in the 2 experiments with different stimulation rates (i.e. 5.88 and 12 Hz) and oddball proportions (1/5 or 1/9), even though the very first (positive) response (100–130 ms) was better isolated in the second experiment. In this second experiment, a comparison to a square wave stimulus presentation revealed that when images were presented sinusoidally, the response was delayed by roughly ¼ of the duration cycle of the sine, i.e. 20 ms in experiment 2. This delay was propagated to subsequent components and remained fixed throughout the entire time course.

The complexity of the response hints at different successive processes involved in rapid facial expression discrimination. This observation agrees with the effects of facial expression reported on multiple ERP components as mentioned in the introduction. However, importantly, here the electrophysiological response identified at the frequency at which a changes of expression appears (*nF*/5 in the first experiment) is not an absolute response to a specific facial expression, but a differential response from neutral faces. Moreover, neutral faces are presented right after the change of expression in the sequence, acting as (backward) masks, so that the prolonged response observed here can only reflect the specific process of the change of facial expression, unlike the components recorded in typical ERP studies. In a similar vein, the vMMN reflects the automatic detection of changes in facial expressions (e.g. Zhao and Li 2006; Astikainen and Hietanen 2009; Stefanics et al. 2012). Yet, in the case of a typical oddball paradigm, the facial expression change is not directly measured (standard and deviant images differ in identity; long SOAs) and the differential response, i.e. the vMMN, has to be isolated through a post hoc subtraction procedure. Here the paradigm appears to provide both a more objective and quantitative response, but also a richer source of information than in typical slow non-periodic oddball studies focusing on the vMMN (Astikainen and Hietanen 2009; Chang et al. 2010).

The detection of expression changes took place very rapidly, around 100 ms and lasted until about 310 ms post-stimulus. The timing of the first positivity is consistent with emergence of emotion category discrimination by 120 ms within the ventral temporal cortex around the fusiform gyrus (i.e. intracranial recordings, Tsuchiya et al. 2008; Kawasaki et al. 2012). Furthermore, quick transitions of images depicting changes in gaze direction or mouth movements have been shown to affect the amplitude of N170 around 200 ms (Puce et al. 1998, 2003; Rossi et al. 2014). As mentioned earlier, these responses originate from activations within the lateral temporal cortex (Puce et al. 1998, 2003). Thus, it is likely that early activation within the ventral and lateral occipito-temporal cortex lead to the early differential responses observed on the scalp here for detecting brief changes of facial expressions. The later positivity observed here may reflect a deeper and more elaborate processing of facial expression discrimination, potentially influenced by feedback projections to the cortex from the amygdala (Vuilleumier et al. 2004).

Conclusions

We provide objective (i.e. frequency-locked) evidence for automatic detection of brief changes in facial expressions in the human brain based on high-level processes. Thanks to the FPVS paradigm, these changes can be detected in single participants and show a high degree of reliability and consistency across individuals. Fearful, disgusted and happy facial expressions are characterized by similar but also specific topographical distribution over the occipito-temporal region, suggesting distributed coding of these expressions within a population of neurons. Quickly transitioning from neutral to expressive faces elicited a rich tri-phasic response from 100 ms to about 310 ms, possibly reflecting specific functional processes that will have to be clarified in future studies. In addition to these new observations, the fast periodic oddball paradigm provides a highly valuable approach to measure discrimination responses due to high-level variations in images. It offers an implicit and reliable measure of detecting brief changes of social cues, in this case facial expressions, significant at an individual level. With its potential to be implemented in clinical practice, the approach opens an avenue for future research exploring rapid perception of social cues in difficult-to-test populations.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org.

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