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## The rapid and automatic categorization of facial expression changes in highly variable natural images

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1           **The Rapid and automatic categorization of facial expression changes in**  
2                                   **highly variable natural images**

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**Declaration of Competing interest**

Declaration of interest: none

32           **Abstract**

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Emotional expressions are quickly and automatically read from human faces under natural viewing conditions. Yet, categorization of facial expressions is typically measured in experimental contexts with homogenous sets of face stimuli. Here we evaluated how the 6 basic facial emotions (*Fear, Disgust, Happiness, Anger, Surprise or Sadness*) can be rapidly and automatically categorized with faces varying in head orientation, lighting condition, identity, gender, age, ethnic origin and background context. High-density EEG was recorded in 17 participants viewing 50 sec sequences with natural variable images of neutral-expression faces alternating at a 6 Hz rate. Every five stimuli (1.2 Hz), variable natural images of one of the six basic expressions were presented. Despite the wide physical variability across images, a significant  $F/5 = 1.2$  Hz response and its harmonics (e.g.,  $2F/5 = 2.4$  Hz, etc.) was observed for all expression changes at the group-level and in every individual participant. Facial categorization responses were found mainly over occipito-temporal sites, with distinct hemispheric lateralization and cortical topographies according to the different expressions. Specifically, a stronger response was found to Sadness categorization, especially over the left hemisphere, as compared to Fear and Happiness, together with a right hemispheric dominance for categorization of Fearful faces. Importantly, these differences were specific to upright faces, ruling out the contribution of low-level visual cues. Overall, these observations point to robust rapid and automatic facial expression categorization processes in the human brain.

*Keywords:* Facial Expression; Natural context; Perception; FPVS; EEG

## 58 1. Introduction

59

60 The ability to quickly and accurately extract one's emotional state from their  
61 face is crucial for social interaction. Ekman (1993) defined six emotions as basic  
62 (*Disgust, Fear, Happiness, Anger, Surprise and Sadness*) which are described as  
63 discrete entities. In line with Darwin's evolutionary work (1872), basic emotions have  
64 been suggested to be universally recognized in the human species through specific  
65 patterns of facial movements called Action-Units (Ekman & Friesen, 1978; but see,  
66 Jack, Blais, Scheepers, Schyns & Caldara, 2009). The perception of these emotional  
67 faces in humans has been studied extensively, for decades, by means of behavioral  
68 (Beaudry, Roy-Charland, Perron, Cormier & Trapp, 2014; Calder, Young, Keane &  
69 Dean, 2000; Palermo & Coltheart, 2004), electrophysiological (Batty & Taylor, 2003;  
70 Caharel, Courtay, Bernard, Lalonde & Rebaï, 2005; Luo, Feng, He, Wang & Luo,  
71 2010) and neuroimaging (Dricu & Frühholz, 2016; Müller-Bardorff et al., 2018;  
72 Wegrzyn et al., 2015) approaches (see Calvo & Nummenmaa, 2016; Vuilleumier &  
73 Pourtois, 2007 for reviews). In most of these studies, decontextualized (i.e.,  
74 segmented) images of faces, usually presented at full-front-views, have been  
75 typically used in order to maximize stimulus control and clarity of facial expressions.  
76 However, in real life situations, emotional expressions have to be quickly and  
77 automatically recognized from faces viewed at different angles, lighting condition or  
78 distance (size). Moreover, facial expressions have to be decoded from individuals of  
79 different ethnicity, gender and age, in extremely variable natural environmental  
80 contexts. While there has been notable increase of studies using natural  
81 heterogenous images of faces to study (familiar) face identity recognition in recent  
82 years (Burton, 2013; Young & Burton, 2017) and influential studies on the role of  
83 (in)congruent contextual scenes on facial expressions (Righart & de Gelder, 2008a,  
84 2008b; Xu, Yang, Tan & Zhang, 2017; for reviews see Aviezer, Ensenberg & Hassin,  
85 2017; Wieser & Brosch, 2012), it is fair to say that the robustness of human facial  
86 expression categorization in highly challenging conditions of variable stimulation  
87 conditions (i.e., heterogenous natural sets of stimuli) remains largely unknown.

88 A promising approach to address this question is Fast Visual Periodic  
89 Stimulation (FPVS) coupled with electroencephalography (EEG), a technique  
90 extended specifically in recent years to provide sensitive measures of (visual) face  
91 categorization (e.g., Rossion, 2014; Rossion, Jacques & Jonas, 2018). FPVS, also

92 called frequency-tagging, is based on the longstanding observation that the periodic  
93 presentation of a stimulus elicits a brain response exactly at the frequency at which  
94 the stimulus is presented, this response being objectively (i.e., at the known  
95 stimulation frequency) captured in the EEG frequency spectrum (Adrian & Matthews,  
96 1934; Regan, 1966; for recent reviews, see Norcia, Appelbaum, Ales, Cottareau &  
97 Rossion, 2015; Rossion, Retter & Liu-Shuang, 2020; Wieser, Miskovic & Keil, 2016).  
98 By means of this approach, Dzhelyova and colleagues (2017) measured the  
99 detection of brief changes of facial expression by presenting the same neutral face  
100 image at a rapid 6 Hz rate (i.e., 6 images/second), with expressive faces of the same  
101 identity appearing every 5 images (i.e., 1.2 Hz). Within a few minutes of visual  
102 stimulation, these changes in facial expressions (from neutral to expressive faces)  
103 elicited significant responses on occipito-temporal sites with specific spatial patterns  
104 of activity according to the emotional expression: the largest ventral occipito-temporal  
105 activity was found for Disgust and Fear, while Happiness elicited a more dorsal  
106 activation (Dzhelyova, Jacques & Rossion, 2017). In subsequent studies, these  
107 results have been replicated with different stimulus sets and extended to the  
108 expressions of Anger and Sadness (Leleu et al., 2018), also showing robust  
109 categorization of a specific expression among each of the other basic expressions  
110 (Luo & Dzhelyova, 2020) or among mixed facial expressions rather than a neutral  
111 face (Poncet, Baudouin, Dzhelyova, Rossion & Leleu, 2019). Despite these  
112 impressive results, rapid automatic categorization of facial expressions across  
113 different identities has not yet been demonstrated with this approach. Most  
114 importantly, highly homogenous sets of visual stimuli, that is, full front faces of human  
115 adults presented out of context and with posed expressions, most often extracted  
116 from databases where the facial features are exaggerated (e.g., “Radboud Faces  
117 Database”: Langner et al., 2010; “Karolinska Directed Facial Expression Database”:  
118 Lundqvist, Flykt & Öhman, 1998; “NimSTIM”: Tottenham et al., 2009) have been  
119 used in the majority of behavioral and neuroimaging studies (but see, for studies  
120 using various environmental contexts: Bublatzki, Kavcıoğlu, Guerra, Doll &  
121 Junghöfer, 2020; Ferrari, Papagno, Todorov & Cattaneo, 2019; Martinez, Falvello,  
122 Aviezer & Todorov, 2015; Xiao, Li, Li & Wang, 2016).

123 Here we extend recent research with the FPVS-EEG approach on  
124 categorization of faces and of familiar face identities with natural (i.e., unsegmented)  
125 variable images (Rossion, Torfs, Jacques & Liu-Shuang, 2015; Rossion et al., 2018;

126 Zimmerman, Yan & Rossion, 2019, respectively) to provide a quantified  
127 electrophysiological measure of the detection of brief changes of facial expressions  
128 with such natural heterogeneous stimulus sets. To do that, we selected natural  
129 emotional faces of the six basic emotions embedded in a naturalistic context: faces of  
130 both children and adult, varying in head orientation, identity, sex, ethnical origin.  
131 Moreover, faces were presented in their original background, which varied within  
132 each emotional category as well as between each of the categories of facial  
133 expression (Fig.1). Despite the high heterogeneity of the stimuli and the challenging  
134 condition of stimulation (i.e., only one glance at a face), we expected robust  
135 automatic categorization responses for all facial expressions tested. Moreover,  
136 considering previous neuroimaging (Harry, Williams, Davis & Kim, 2013; Wegrzyn et  
137 al., 2015; Zhao, Zhao, Zhang, Cui & Fu, 2017) and electrophysiological results  
138 (Brenner, Rumak, Burns & Kieffaber, 2014; Campagnoli et al., 2019; Dzhelyova et  
139 al., 2017; Turano et al., 2017), these categorization responses were expected  
140 primarily over occipito-temporal regions, with higher neural responses for negative  
141 than positive expressions (Batty & Taylor, 2003; Caharel et al., 2005; Vytal &  
142 Hamann, 2010; Whalen et al., 2013). Larger categorization responses were also  
143 expected over the right hemisphere, in line with the dominance of this hemisphere in  
144 facial expression categorization and face recognition in general (Calvo & Beltrán,  
145 2014; Hillger & Koenig, 1991; Jacques & Rossion, 2009; Rossion, Dricot, Goebel &  
146 Busigny, 2011; Sergent, 1988; Sergent, Ohta & MacDonald, 1992), and as previously  
147 observed in FPVS-EEG studies (Dzhelyova et al., 2017; Leleu et al., 2018). Finally,  
148 the specific contribution of high-level categorization processes, i.e., going beyond  
149 physical image cues, was isolated by comparing these responses to the exact same  
150 images presented upside-down, expecting a substantial decrease of response in this  
151 stimulation condition.

152

## 153 **2. Materials and Methods**

154 We report how we determined our sample size, all data exclusions, all  
155 inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior  
156 to data analysis, all manipulations, and all measures in the study.

## 157 **2.1. Participants**

158 Seventeen participants (7 males, mean age = 23.16, SD = 2.24, range =  
159 19.25-27.5; all right-handed) provided signed and informed consent and were paid  
160 for their participation in the experiment, which was approved by the ethical committee  
161 of the University of Louvain. The sample size was established according to previous  
162 FPVS-EEG studies (e.g., Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al.,  
163 2018), considering that this approach is characterized by a very high signal-to-noise  
164 ratio (SNR) (Norcia et al., 2015; Regan, 1989). This high SNR is partly due to the  
165 large number of categorization responses measured (i.e., here 60 changes of facial  
166 expressions in a stimulation sequence, resulting in 240 trials for the 4 repetitions of  
167 each condition, as described below). All participants reported normal or corrected-to-  
168 normal vision. None of the participants reported any history of psychiatric or  
169 neurological disorders.

170

## 171 **2.2. Stimuli**

172 One hundred images of natural facial expressions were selected on the basis  
173 of a pilot experiment carried out on a large set of images collected on the internet (n=  
174 303). The faces in the selected images for the experiment varied in head orientation,  
175 lighting direction, identity, age, sex, ethnical origin, and surrounding background.  
176 These stimuli were rated by an independent group of participants (n = 23, mean age  
177 = 21.23, SD = .19, range = 20.01 – 23.10). In that pilot study, participants were asked  
178 to categorize the displayed expression in a seven-alternative forced-choice task  
179 (*Disgust, Fear, Happiness, Anger, Sadness, Surprise, Neutral and undefined*) and  
180 evaluate its intensity on a scale ranging from 1 (low intensity) to 9 (very high  
181 intensity). In order to select the stimuli, a cut-off of 70% for each image was used as  
182 the lower recognition rate. Based on this criterion but also on the matching of the  
183 stimuli according to their intensity rating, forty face images corresponding to a neutral  
184 expression and ten images for each basic emotion (*Disgust, Fear, Happiness,*  
185 *Surprise, Anger and Sadness*) were selected (see Table 1). For these remaining  
186 images, the hit rate was very high (mean hit rates = 91.83 %, SD = 6.00). Repeated-  
187 measures analysis of variances (ANOVA) with *Emotion (Disgust, Fear, Happiness,*  
188 *Anger, Surprise, Sadness and Neutral)* as within-subject factor were conducted both  
189 for hit rates and intensity ratings on this image set. A significant effect of emotion was  
190 observed on intensity ratings ( $F(6, 132) = 4.21, \epsilon = .42, p = .01, \eta_p^2 = .16$ ). Post-hoc

191 analyses with Bonferroni correction for multiple comparisons showed that the neutral  
 192 expression was less intense than Fear, Happiness, Sadness and Surprise  
 193 (respectively  $p = .0017$ ,  $p = .003$ ;  $p = .0057$  and  $p = .003$ ). The main effect of emotion  
 194 on hit rates was also significant ( $F(6, 132) = 6.96$ ,  $\epsilon = .54$ ,  $p = .0003$ ,  $\eta_p^2 = .24$ ), due  
 195 to Fear being less well recognized than Anger ( $p = .03$ ), Happiness ( $p < .0001$ ),  
 196 Sadness ( $p = .003$ ) and Surprise ( $p = .03$ ). Also, neutral faces were less well  
 197 recognized than happy ( $p = < .0001$ ) and sad ( $p = .006$ ) faces. This observation is  
 198 consistent with previous studies with homogenous image sets showing that Fear is  
 199 less well recognized and often confused with Surprise (e.g., Tracy & Robins, 2008).  
 200

	<b>Fear</b>	<b>Disgust</b>	<b>Happiness</b>	<b>Sadness</b>	<b>Anger</b>	<b>Surprise</b>	<b>Neutral</b>
Hit rates (%) (SD)	83.48 (16.64)	91.74 (10.72)	99.57 (2.09)	96.09 (7.22)	94.91 (7.83)	93.91 (10.33)	84.13 (15.61)
Intensity (SD)	7.14 (1.10)	6.79 (1.55)	7.11 (1.14)	7.07 (1.19)	6.92 (1.35)	7.11 (1.17)	6.25 (2.01)

201  
 202 **Table 1. Behavioral rating of natural images. Mean hit rate (SD) and mean intensity (SD) for**  
 203 **selected images for each emotional expression category.**

204  
 205 **2.3. Procedure**

206 2.3.1. EEG testing

207 The procedure was similar to a previous study (Dzhelyova et al., 2017) using  
 208 fast periodic visual stimulation (FPVS) to identify a neural signature to facial  
 209 expression categorization. After electrode cap placement, participants were seated in  
 210 a dimly lit room, at a viewing distance of 80 cm from a computer monitor (LED screen  
 211 (BenQXL2420T) with a 1920 x 1080 pixels resolution and a 120 Hz refresh rate).  
 212 During stimulation, stimuli appeared in the center of a uniform light gray background  
 213 and displayed with 383 pixels x 383 pixels resolution and a size of 7.249 x 7.249  
 214 degrees of visual angle at this distance. During the experiment, a fixation cross was  
 215 displayed in the center of the images and the participants were instructed to press  
 216 the “space bar” when they noticed a brief and random color change of the fixation  
 217 cross from blue to red (lasting 200 msec, 12 times during a sequence). This



218 orthogonal task ensured that participants paid attention to the screen during the  
219 sequence.

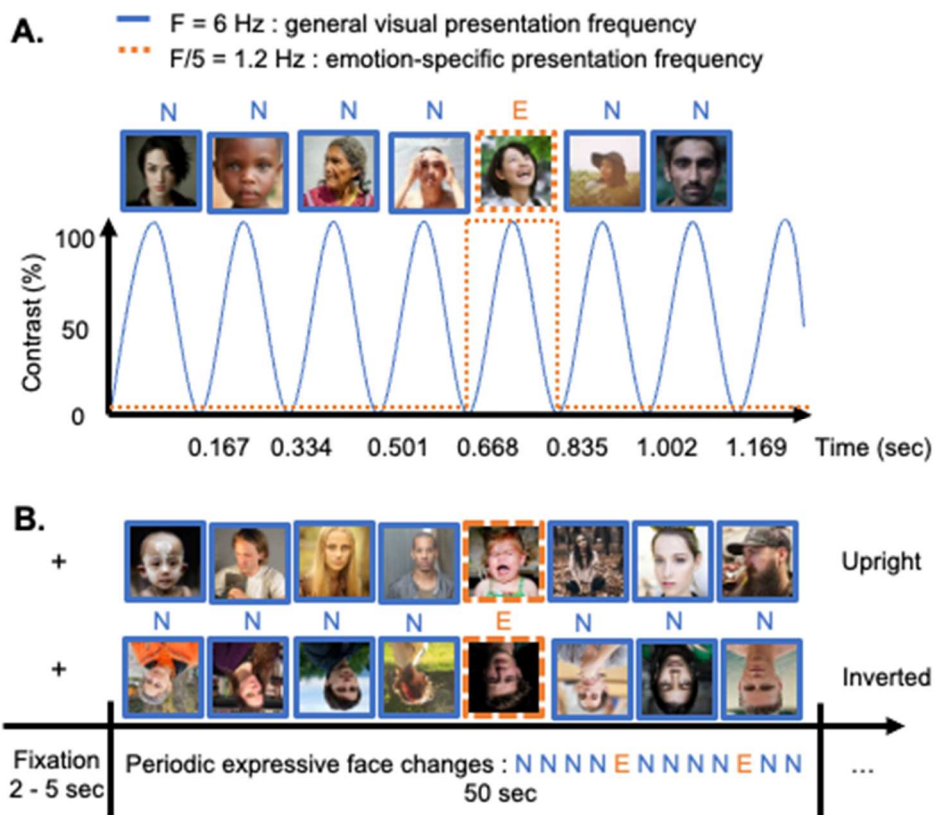
220 Each sequence started with a variable duration of 2-5 sec of a blank screen, 2  
221 sec of gradually fading in of the stimuli presentation, followed by 50 sec of stimulation  
222 sequence and 2 sec of gradually fading out of the stimuli. Images were presented at  
223 a base rate stimulation of 5.9991 Hz (i.e., approximately 6 images per second, image  
224 presentation duration  $\approx$  167 msec) with the constraint that every fifth images an  
225 emotional expression was presented (expression-specific rate =  $6/5 = 1.2$  Hz),  
226 resulting in a sequence  $N_{\text{Neutral}} N_{\text{Neutral}} N_{\text{Neutral}} N_{\text{Neutral}} E_{\text{Expressive}} N_{\text{Neutral}} N_{\text{Neutral}} N_{\text{Neutral}} N_{\text{Neutral}}$   
227  $E_{\text{Expressive}}$  (see Fig. 1). For each sequence, different individuals with a neutral  
228 expression were randomly selected as the base face (N) and different individuals with  
229 a given emotional expression (E) were randomly inserted at the expression-specific  
230 rate. Images were presented through a sinusoidal contrast modulation (0-100%).  
231 Each pixel of the images reached the full luminance value of the face stimulus after  
232 half a cycle, approximately 83 msec after the stimulus onset ( $((1000/6)/2)$ ). A practical  
233 advantage of the sine mode of stimulation is that it is a smoother stimulation than the  
234 square wave stimulation and it is defined with a single parameter (stimulus onset  
235 asynchrony (SOA) or rate). Another advantage is that the visual stimulation is present  
236 almost all the time, thus giving a continuously changing percept.

237 In order to respect equiprobability presentation of the pictures, the entire set of  
238 images was repeated 6 times within every sequence ( $6 \text{ Hz} \times 50 \text{ sec} = 300$  pictures  
239 presented during each sequence, including 60 expressive faces ( $= 300/5$ ) and 240  
240 neutral faces). In order to control for low-level effects, each sequence, assessing the  
241 discrimination of one specific emotional expression compared to neutral faces, was  
242 presented both at upright and inverted orientations. The presence of an inverted face  
243 condition was motivated by the fact that, while images-based cues are preserved by  
244 inversion, high-level processing of faces, including facial expression processing, is  
245 impaired by this manipulation of orientation (e.g.; Calvo & Nummenmaa, 2008;  
246 Farah, Tanaka & Drain, 1995; Van Belle, Graef, Verfaillie, Rossion & Lefèvre, 2010).  
247 In total, twelve conditions were implemented: 6 emotional expressions (Disgust, Fear,  
248 Happiness, Surprise, Anger and Sadness) and 2 orientations (upright or inverted).  
249 Each condition was repeated 4 times, resulting in 48 sequences. 8 blocks of 6  
250 sequences were created corresponding to each emotional expression (one

251 orientation per block). Blocks' and sequences' order were randomized for every  
 252 participant.

253 By presenting faces at 6 Hz, we expected an EEG response at 6 Hz and at  
 254 harmonics (i.e., 12 Hz, 18 Hz etc.) reflecting the general visual responses to the  
 255 images. In order to quantify the discrimination response to emotional expressions,  
 256 only frequencies corresponding to the presentation rate of the expressive faces were  
 257 considered, namely the expression-specific frequency ( $F/5 = 1.1998$  Hz, rounded to  
 258 1.2 Hz) and its harmonics (i.e.  $2F/5 = 2.3996$  Hz,  $3F/5 = 3.5994$  Hz,  $4F/5 = 4.7992$   
 259 Hz, rounded to 2.4 Hz, 3.6 Hz and 4.8 Hz respectively).

260



261

262 **Fig. 1. Stimuli and experimental design.** A. Example of a sequence with neutral  
 263 expression faces at the base rate (6 Hz – blue line) with the constraint that every five faces an  
 264 emotional expression, Happiness in this example, was periodically inserted at the expression-  
 265 specific rate of 1.2 Hz ( $6 \text{ Hz}/5 = 1.2 \text{ Hz}$  – orange dotted line). B. Each sequence started with a  
 266 fixation cross presentation which varied between 2-5 seconds, followed by a 2 seconds fade-in,  
 267 50 sec of stimuli presentation and finished with a 2 seconds fade-out. Each sequence was  
 268 presented with two orientations (upright and inverted faces) and presented four times,  
 269 resulting in 48 sequences (2 orientations; 6 expressions – *Disgust, Fear, Happiness, Surprise,*  
 270 *Anger and Sadness* - and four repetitions).

271

### 272 2.3.2. EEG acquisition

273 Scalp electroencephalographic (EEG) activity was recorded using a 128-  
274 channels BIOSEMI Active-Two (the common mode sense active electrode was used  
275 as reference and the driven right leg passive electrode was used as ground) system  
276 (BioSemi, Amsterdam, Netherlands), including both standard 10–20 system locations  
277 and additional intermediate positions. Electrode offset was reduced 30  $\mu$ V for each  
278 individual electrode. Eye-movements were monitored with 4 external electrodes,  
279 included 2 electrodes for vertical eye movements placed above and below the right  
280 eye and 2 electrodes for horizontal eye movements placed at the corner of each eye.  
281 Continuous EEG was sampled at 512 Hz.

282

## 283 **2.4. EEG Analysis**

284

285 All EEG processing steps were carried out using Letswave 5  
286 (<http://nocions.webnode.com/letswave>), and Matlab R2014a (The Mathworks).

287

### 288 2.4.1. Preprocessing

289 The continuously recorded data were first filtered using a bandpass filter at  
290 0.1-120 Hz (Butterworth filter, fourth order) and then resampled to 256 Hz to save  
291 disk space and reduce computational load. The data were then cropped into 56 sec  
292 segments (4 sec before and 2 sec after each stimulation sequence corresponding to  
293 the 2 sec fading in, 2 sec fading out and 2 extra sec). For 5 participants who blinked  
294 on average above 0.1 times/sec (average number of blinks across participants = 0.1,  
295 SD = 0.07), blinks were corrected by means of independent component analysis  
296 (ICA) using the runica algorithm (Bell & Sejnowski, 1995; Makeig, Bell, Jung &  
297 Sejnowski, 1996), as implemented in EEGLAB. This algorithm outputs a square  
298 mixing matrix in which the number of components corresponds to the number of  
299 channels. For each of these 5 participants, only the first component, accounting for  
300 most of the variance, representing vertical eye movements was removed. Next, noisy  
301 or artifact ridden channels (not more than 5% of the electrodes) were re-estimated  
302 using linear interpolation of the 3 nearest spatially neighboring electrodes, (on

303 average, 1.8 electrodes were interpolated). All data segments were re-referenced to a  
304 common average reference.

305

#### 306 2.4.2. Frequency-domain analysis

307 Preprocessed data segments were cropped down to an integer number of 1.2  
308 Hz cycles beginning immediately after the fade in, until approximately 49.18 sec ( $\approx$  50  
309 sec, 59 cycles, 12589 time bins in total) in order to separate each condition. Data  
310 were then averaged in the time domain, separately for each condition: Orientation  
311 (Upright, Inverted) and Facial Expression (Disgust, Fear, Happiness, Surprise, Anger,  
312 Sadness) and for each participant. A Fast Fourier Transformation (FFT) was then  
313 applied to these averaged segments and amplitude spectra were extracted for all  
314 channels. The FFT transformation yielded a spectrum ranging from 0 to 256 Hz with  
315 a high spectral resolution of about 1/49 s, i.e. 0.02 Hz. Z-scores were calculated on  
316 the FFT grand-averaged data pooled across all electrodes for each condition in order  
317 to assess the significance of the responses at different harmonics. Z-scores were  
318 computed as in a previous study, using the mean and the standard deviation of the  
319 20 frequency bins surrounding the frequency of interest (excluding the immediately  
320 neighboring bin and the 2 most extreme value, e.g. Liu-Shuang, Norcia & Rossion,  
321 2014), resulting in 10 bins in each side. For the following analyses, we considered for  
322 the expression-specific response all consecutive harmonics that were significant with  
323 a Z-score above 2.32 ( $p < .01$ , one tailed, i.e. signal  $>$  noise) in at least one condition  
324 since one might expect differences in the strength of the discrimination responses  
325 depending on the facial expression. For the base rate response, reflecting the  
326 general visual processing of the faces, as we expected no differences for the different  
327 expression discriminations, harmonics were considered as significant until the Z-  
328 score was no longer above 2.32 ( $p < .01$ ) for all the conditions. Based on this  
329 criterion, the expression-specific response was quantified as the sum of the  
330 expression-specific response harmonics (Retter, Rossion & Schiltz, in press) until the  
331 8<sup>th</sup> harmonic (i.e.  $8F/5 = 9.598$  Hz, rounded 9.6 Hz, excluding the 5<sup>th</sup> harmonic  
332 corresponding to the base frequency rate  $F = 6$  Hz). The response at the base  
333 frequency rate was quantified as the sum of the base rate until the 5<sup>th</sup> harmonic (i.e.  
334  $5F = 30$  Hz) (see Figs. 2A and 2B).

335 SNR and baseline-corrected amplitude were used to describe the response at  
336 the frequency of interest. SNR was computed as the amplitude value at the bin of

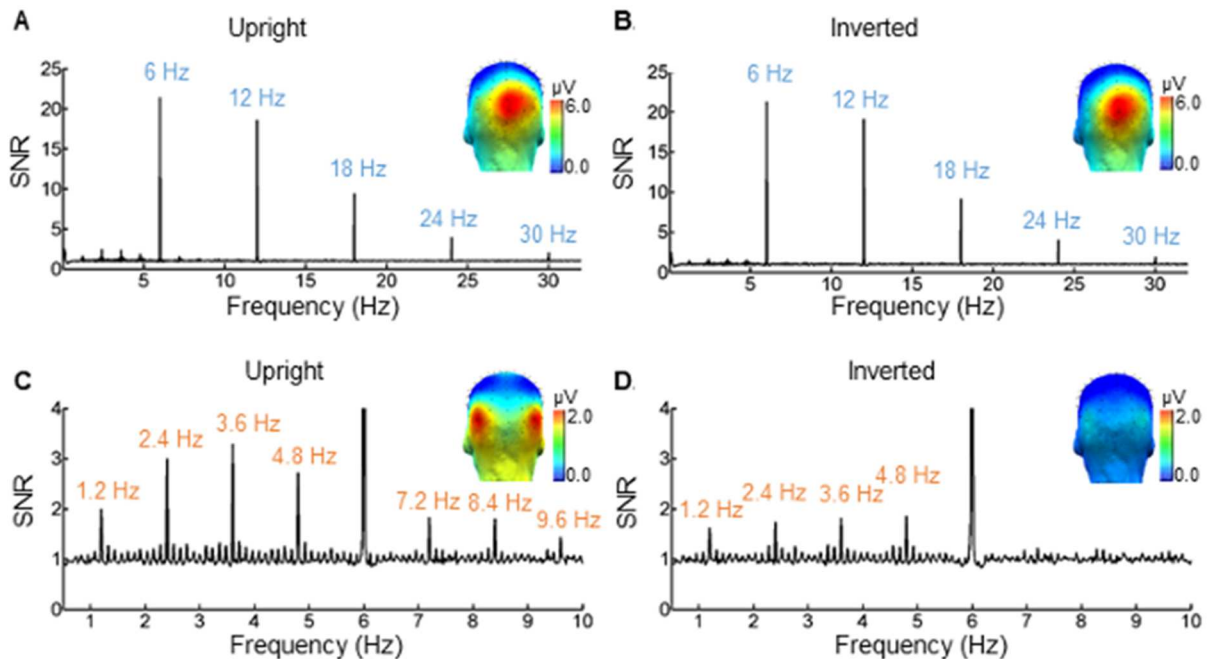
337 interest divided by the average amplitude of the 20 surrounding frequency bins  
338 (excluding the 2 most extreme bins and the immediately neighboring bin, resulting in  
339 10 bins in each side, e.g. Liu-Shuang et al., 2014). SNR spectra were used for data  
340 visualization, since the harmonic responses at high frequency ranges may be of  
341 small amplitude but with a high SNR. In order to combine expression-specific  
342 response harmonics (i.e.  $f/5 = 1.2$  Hz;  $2f/5 = 2.4$  Hz etc.), we first applied a baseline-  
343 correction to the amplitude by subtracting the average noise level of the surrounding  
344 20 bins and then summed the baseline-corrected amplitudes 8 expression-specific  
345 frequency harmonics (see Figs. 2C and 2D).

346 For the group analysis, grand-averages of the SNR and baseline-corrected  
347 amplitudes were computed across participants for each condition and electrode  
348 separately. In order to better visualize hemispheric differences for each emotion, we  
349 cropped the FFT spectrum in different epochs, centered at the expression-specific  
350 response (1.2 Hz and the subsequent harmonics until 9.6 Hz), surrounded by 10  
351 neighboring bins, representing the noise level. Then, we summed the epochs  
352 corresponding to the expression-specific frequencies excluding 5<sup>th</sup> epoch  
353 corresponding to the base rate (6 Hz). Similarly, for the general visual response, we  
354 cropped the FFT spectrum in different epochs, centered this time at 6 Hz and the 5  
355 harmonics, surrounded by 10 neighboring bins, and summed these epochs. We  
356 applied a baseline-correction by subtracting the average noise level of the  
357 surrounding 10 bins excluding the immediately adjacent and the maximal ones. To  
358 visualize data at the group level, we average each condition and electrode  
359 separately. Then, we averaged for each expression changes the electrodes  
360 corresponding to the ROI defined below.

361 For the statistical analysis, based on previous research (Dzhelyova et al.,  
362 2017; Leleu et al., 2018) and visual inspection of topographical maps, we determined  
363 regions of interest (ROIs). Each ROI corresponded to the pooling of the four channels  
364 with the strongest activation. Thereby, we defined, for general visual response one  
365 medial ROI comprising the medial occipital (mO) sites (mO: Oz, Olz, Iz and O2) and  
366 for expression-specific response 2 ROI, the left and right posterior-occipital (IOT;  
367 rOT) sites (P9, PO7, PO9, PO11 and P10, PO8, PO10, PO12 respectively).

368 Repeated-measures analysis of variances (ANOVA) were conducted on the  
369 baseline-corrected amplitudes with *Expression* (Disgust, Fear, Happiness, Surprise,  
370 Anger, Sadness), *Orientation* (Upright, Inverted) and *ROI* as within factors.

371 Greenhouse-Geisser correction were applied to adjust degrees of freedom wherever  
 372 the assumption of sphericity was violated (corresponding to the epsilon ( $\epsilon$ ) values).  
 373 For significant effects or interactions, post-hoc comparisons were performed using  
 374 Bonferroni adjustment. Effect size was estimated with partial  $\eta^2$ . The alpha  
 375 significance value used was 0.05.



376  
 377 **Fig. 2. Grand-average EEG spectra in SNR of all emotional expressions (average across**  
 378 **Disgust, Fear, Happiness, Surprise, Anger and Sadness).** The upper part of the figure  
 379 represents neural response to the base rate (6 Hz) and its significant harmonics (2F = 12 Hz, 3F  
 380 = 18 Hz, 4F = 24 Hz and 5F = 30 Hz) over a medial occipital region extending slightly to right  
 381 occipito-temporal region of interest (ROI) (averaged across Oz, Olz, Iz and O2 channels),  
 382 shown separately for A. upright faces and B. inverted faces. Lower part of the figure represents  
 383 emotional-specific response (F/5 = 1.2 Hz) and its significant harmonics (2F/5 = 2.4 Hz, 3F/5 =  
 384 3.6 Hz, 4F/5 = 4.8 Hz, 6F/5 = 7.2 Hz, 7F/5 = 8.4 Hz and 8F/5 = 9.6 Hz) over occipito-temporal ROI  
 385 (averaged across left and right occipito-temporal channels, P9, PO7, PO9 and PO11 and P10,  
 386 PO8, PO10 and PO12 respectively), shown separately for C. upright and D. inverted faces. 3D-  
 387 topographic scalp maps (posterior view) on the average of all emotions and significant  
 388 responses (same scale for both orientations, ranging from 0 to 6  $\mu$ V for the general visual  
 389 responses (A. and B.) and ranging from 0 to 2  $\mu$ V for the expression-specific responses (C. and  
 390 D.) showed the distinct scalp distribution.

391  
 392 2.4.3. Individual Analysis

393 The response to facial expression was also evaluated at the individual level for  
 394 upright faces. In order to visualize the overall response for each individual participant,  
 395 we cropped the FFT spectrum in different epochs, centered at the expression-specific

396 response (1.2 Hz and the subsequent harmonics until 9.6 Hz), surrounded by 10  
397 neighboring bins, representing the noise level. Then, we summed the epochs  
398 corresponding to the expression-specific frequencies excluding the 5<sup>th</sup> epoch  
399 corresponding to the base rate (6 Hz). For each participant and condition, we  
400 computed an average of responses in each of the ROI defined at the group level  
401 (PO7, PO9, PO11, P9 and PO8, PO10, PO12, P10 for the left and right hemisphere  
402 respectively). Then, we calculated Z-scores on the FFT spectrum (see group level  
403 analysis for the method) in order to assess the significance of the responses in both  
404 ROIs for each expression at the individual level. We also applied a baseline-  
405 correction by subtracting the average noise level of the surrounding 10 bins  
406 excluding the immediately adjacent and the maximal ones. Interhemispheric  
407 differences for each expression were estimated by pairwise *t*-tests to compare left  
408 and right ROI amplitude per participants.

409

#### 410 2.4.4. Brain topographical analysis

411 Previous studies (Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al.,  
412 2019) showed distinct brain responses according to the facial expression in the  
413 occipito-temporal regions. However, to examine potential topographical differences,  
414 individual baseline-corrected FFT spectrum data for each facial expression in upright  
415 and inverted orientation were normalized. For each participant, the baseline-  
416 corrected spectrum for each condition was first scaled by dividing the value at each  
417 electrode by the scalp-wide root-mean-square value (i.e. the square root of the sum  
418 of squares for all the 128 electrodes) (McCarthy & Wood, 1985). These normalized  
419 amplitudes were then summed for the significant harmonics. Normalized amplitudes  
420 were used for this analysis to ensure that topographical differences are not driven by  
421 amplitude differences between conditions. A mass univariate test was then used to  
422 estimate the effects of Expression (Disgust, Fear, Happiness, Surprise, Anger and  
423 Sadness) for each orientation on the 128 electrode sites. To this end, 10 000 random  
424 permutations were computed and for each permutation, an ANOVA test was  
425 conducted. Then, for each permutation, we stored the absolute maximum F-value in  
426 order to create the empirical F-distribution for our experiment. The 0.05 tails of this  
427 distribution were later used for determining statistical significance. The described  
428 method has been shown to provide a highly conservative threshold controlling for  
429 multiple comparison (Groppe, Urbach & Kutas, 2011). Significant differences

430 between experimental conditions at one of the electrode sites were followed by a  
431 Bonferroni post hoc analysis.

432

#### 433 2.4.5. Time-domain analysis

434 In order to visualize the shape of the periodic changes time-locked to the  
435 emotional expression stimulus and estimate the speed and time course of facial  
436 expression changes, we performed time-domain analysis. Preprocessed and re-  
437 referenced data were low-pass FFT filtered at 30 Hz. A FFT notch filter with 0.05  
438 width selectively removed the dominating base frequency, 6 Hz and its harmonics  
439 (i.e., 12Hz, etc.). The first and last 2 sec of the sequence corresponding to the fade in  
440 and fade out were excluded. Overlapping, locked to the expression-specific  
441 presentation epochs were segmented, lasting for an overall duration of 2000 msec  
442 (12 cycles of the base rate). For each sequence, 57 epochs were available per  
443 repetition for each condition (57 expression-specific images x 833 msec per cycle =  
444 47 510 msec). These epochs were averaged for each participant and baseline-  
445 corrected by subtracting the signal within the 167msec pre-stimulus presentation,  
446 corresponding roughly to 1 cycle of the base rate. A *t*-test comparing when the  
447 waveforms were significantly different from 0 ( $p < .05$ , for at least 5 consecutive  
448 points, approximately 20 msec) was performed.

449

### 450 3. Results

#### 451 3.1. Behavioral Data of the Change of Fixation Color Task

452 Repeated-measures analysis of variances (ANOVA) with *Orientation* (Upright,  
453 Inverted) and *Facial Expression* (Anger, Disgust, Fear, Happiness, Sadness,  
454 Surprise) as within-subject factors indicated no differences in task performance  
455 between upright and inverted faces (accuracy:  $F(1, 16) = 1.04, \epsilon = 1.00, p = .32$ ;  
456 Response Times (RTs):  $F(1, 16) = 2.65, \epsilon = 1.00, p = .12$ ) as well as between the  
457 different facial expressions (accuracy:  $F(5, 80) = 1.01, \epsilon = .72, p = .41$ ; RTs:  $F(5, 80)$   
458  $= .76, \epsilon = .43, p = .48$ ). The interaction between Orientation and Facial Expression  
459 also did not reach significance (accuracy:  $F(5, 80) = .98, \epsilon = .70, p = .42$ , RTs:  $F(5,$   
460  $80) = .78, \epsilon = .39, p = .46$ ).

461



## 462 **3.2. EEG Data: Frequency Analysis**

### 463 3.2.1. Base Frequency: General Visual Stimulation

464 Although it was not the main purpose of this study, we analyzed the responses  
465 obtained at the base rate frequency, reflecting the general response of the visual  
466 system of the stimulation. There were robust responses at this frequency, with larger  
467 responses over medial occipital sites, extending slightly towards the right lateral  
468 occipital sites (see Figs. 2A and 2B). In order to evaluate the effects of *Orientation*  
469 and *Expression* at the base rate frequency in these regions, we performed repeated  
470 measures ANOVAs on the summed baseline corrected amplitudes over the medial  
471 occipital region (mO: Oz, Olz, Iz and O2) (sum of the 5 base rate harmonics (i.e.,  
472 until 29.99 Hz over these sites). A main effect of *Facial Expression* was revealed,  
473  $F(5, 80) = 4.08$ ,  $\epsilon = .696$ ,  $p = .008$ ,  $\eta p^2 = .20$ , due to a lower response for Sadness  
474 compared to Happiness and Anger, irrespectively of orientation ( $p = .005$  and  $p =$   
475  $.004$ , respectively). However, neither the effect of *Orientation* ( $F(1,16) = .008$ ,  $\epsilon =$   
476  $1.00$ ,  $p = .931$ ), nor the interaction between *Orientation* and *Expression* ( $F(5,80) =$   
477  $.56$ ,  $\epsilon = .74$ ,  $p = .68$ ), were significant.

478

### 479 3.2.2. Expression-specific Frequency: Discrimination of Emotional Expression

480 Despite the heterogeneity and the brevity of the image presentation,  
481 responses corresponding to the frequency of expression change (from a neutral face  
482 to an expressive face) were clearly observable at 1.2. Hz and its harmonics (see  
483 Figs. 2C and D). Scalp topographies of the summed responses of the first 8  
484 harmonics (i.e.,  $f/5$ ;  $2f/5$  etc., until 9.6 Hz excluding the base rate) (see Fig. 3)  
485 showed that the expression-specific responses were larger on the occipito-temporal  
486 regions. In addition, interhemispheric differences in these regions emerged according  
487 to the different types of expression change.

488 While the change from a neutral to a fearful or happiness expression seemed  
489 to engage mainly the right hemisphere, a change to a sad expression seemed to  
490 further engage the left hemisphere (see Fig. 3). The other changes, especially  
491 changes to Disgust, Surprise and Anger, seemed to be bilaterally distributed.  
492 Interestingly, among all the expressions used, the largest response was observed for  
493 faces expressing Sadness. Moreover, these occipito-temporal activities were

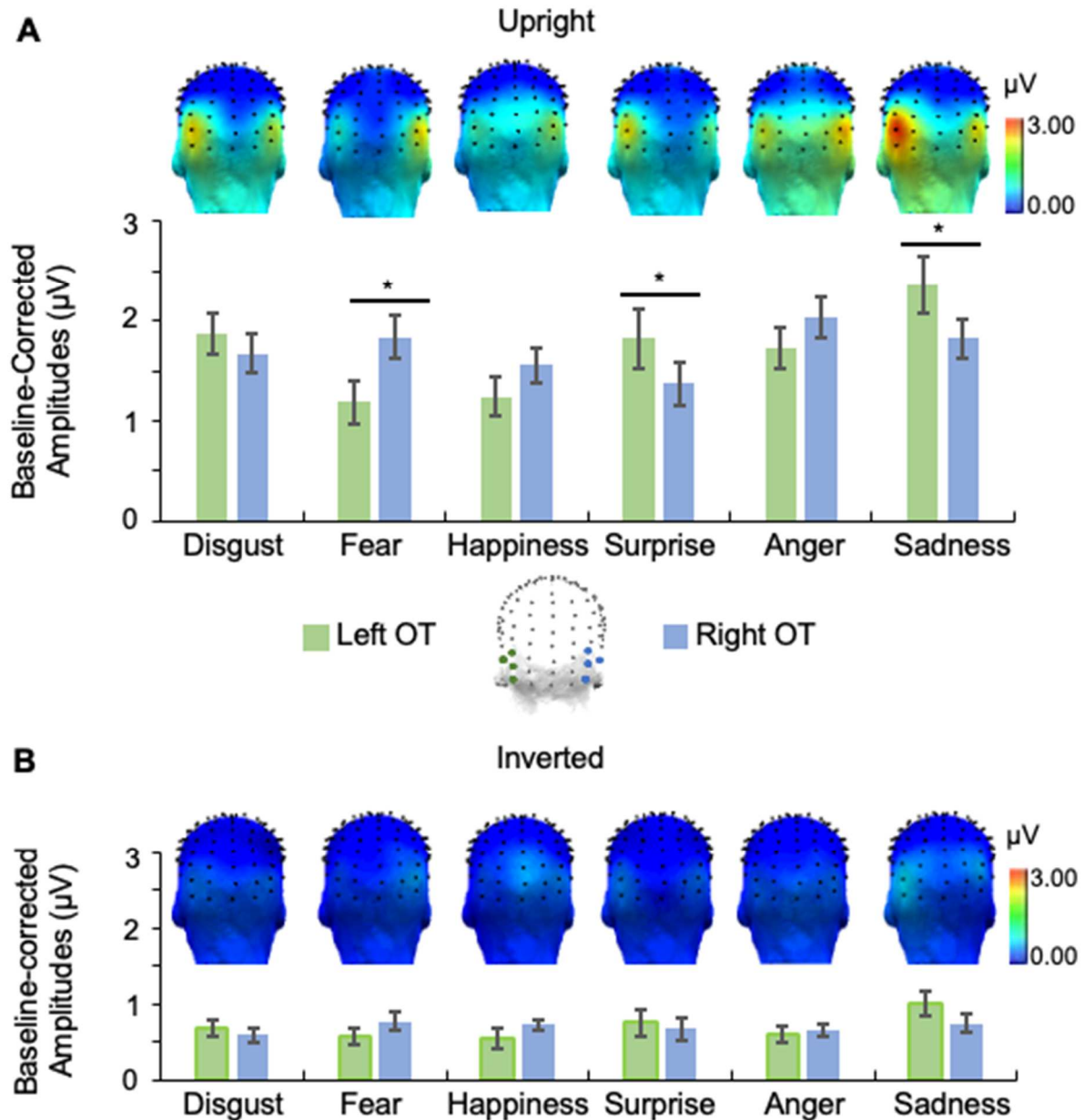
494 reported only for upright faces, thus confirming that face inversion strongly disrupts  
495 the processing of emotional expressions (see Fig. 3).

496

### 497 3.2.2.1. Response over the whole scalp

498 To test these observations without predefined ROIs, a repeated-measures  
499 ANOVA was first carried out on the grand-averaged summed baseline-corrected  
500 amplitudes across all the 128 channels response with *Orientation* and *Facial*  
501 *Expression* as within-subject factors. This analysis revealed a main effect of both  
502 *Facial Expression*,  $F(2, 80) = 3.62$ ,  $\epsilon = .62$ ,  $p = .018$ ,  $\eta_p^2 = .18$  and *Orientation*,  $F(1,$   
503  $16) = 56.77$ ,  $\epsilon = 1.00$ ,  $p < .0001$ ,  $\eta_p^2 = .78$ . The interaction between *Orientation* and  
504 *Facial Expression* was also significant,  $F(5, 80) = 3.62$ ,  $\epsilon = .795$ ,  $p = .01$ ,  $\eta_p^2 = .18$ ,  
505 and was explained by a significant effect of *Facial Expression* only for upright  
506 orientations (Upright:  $F(5,80) = 4.16$ ,  $\epsilon = .64$ ,  $p = .009$ ,  $\eta_p^2 = .002$ ; Inverted:  $F(5,80) =$   
507  $2.24$ ,  $\epsilon = .81$ ,  $p = .07$ ). This last effect was due to higher amplitudes for changes to  
508 Anger than changes to Fear and to Happiness ( $p = .018$  and  $p = .01$ , respectively).

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**Fig. 3.** Neural responses to expression-specific frequency for A. upright and B. inverted faces. The sum of baseline-corrected amplitudes (in  $\mu\text{V}$ ) of the expression-specific response and its significant harmonics (until 8F/5, i.e. 9.6 Hz, excluding the base rate at 6 Hz) over left (average across P9, PO7, PO9, PO11 channels; green bars) and right (average across P10, PO8, PO10, PO12 channels; blue bars) occipito-temporal regions plotted separately for each facial expression (respectively left OT and right OT). Error bars are standard errors of the mean (SEM). \* indicates a significant difference between left and right ROI for the concerned emotional expression. Scalp topographies (in  $\mu\text{V}$ ) shown for each expression (*Disgust*, *Fear*, *Happiness*, *Surprise*, *Anger* and *Sadness*) separately with the same scale (from 0 to 3.00  $\mu\text{V}$ ) for the summed baseline-corrected amplitude of the 1.2 Hz response and its subsequent significant harmonics. Neural responses to emotional expression are largely reduced for inverted faces compared to upright faces.

### 524 3.2.2.2. ROI Analysis

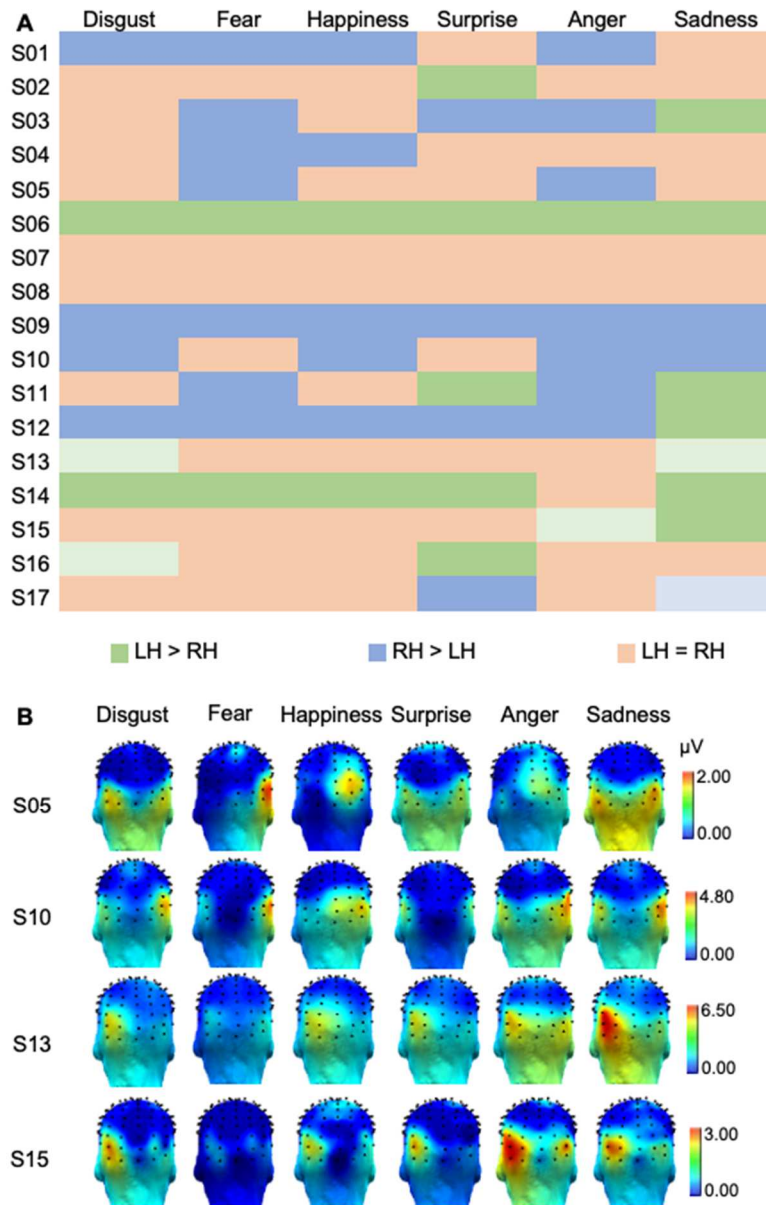
525 Since the discrimination response to emotional expression was distributed  
526 mainly over the occipito-temporal sites, two main regions of interest in the right and  
527 the left hemisphere were defined for further analysis. Each ROI comprised 4  
528 electrodes, P9, PO7, PO9 and PO11 for the left hemisphere and the corresponding  
529 electrodes in the right hemisphere (see Fig. 3). Thus, as above, a repeated-  
530 measures ANOVA was carried out on the amplitudes by adding the ROI, left and right  
531 occipito-temporal sites (IOT; rOT), as a factor. This analysis revealed that the  
532 expression-specific response was larger for upright than for inverted orientations,  
533  $F(1, 16) = 90.31$ ,  $\epsilon = 1.00$ ,  $p < .0001$ ,  $\eta_p^2 = .85$ . The amplitudes were also significantly  
534 different among the 6 expressions, regardless of their orientation,  $F(5, 80) = 4.6$ ,  $\epsilon =$   
535  $.52$ ,  $p = .0095$ ,  $\eta_p^2 = .22$ . However, the main effect of *ROI* did not reach significance,  
536  $F(1,16) = 0.10$ ,  $\epsilon = 1.00$ ,  $p = .76$ . More interestingly, the two-way interactions with  
537 *Facial Expression* reached significance (*Expression x ROI*:  $F(5,80) = 17.09$ ,  $\epsilon = .796$ ,  
538  $p < .0001$ ,  $\eta_p^2 = .52$ , and *Expression x Orientation*:  $F(5, 80) = 2.94$ ,  $\epsilon = .66$ ,  $p = .037$ ,  
539  $\eta_p^2 = .16$ ) as well as the 3-way interaction between *Expression*, *Orientation* and *ROI*,  
540  $F(5,80) = 4.96$ ,  $\epsilon = .53$ ,  $p = .006$ ,  $\eta_p^2 = .24$ . This last interaction was explained by the  
541 same level of activity in left and right hemisphere ( $p > .05$ ) for inverted faces.  
542 However, for upright faces, higher responses were measured in the right hemisphere  
543 for Fear expressions ( $p < .0001$ ) and in left hemisphere for sad ( $p = .002$ ) and  
544 Surprised ( $p = .02$ ) faces. Interhemispheric differences for the other expressions did  
545 not reach significance ( $ps > .05$ ) (see Fig. 3). Additionally, regardless of the ROI, the  
546 main effect of Expression was significant only for upright orientation (*Upright*:  $F(5,80)$   
547  $= 4.63$ ,  $\epsilon = .56$ ,  $p = .008$ ,  $\eta_p^2 = .22$ ; *Inverted*:  $F(5,80) = 1.86$ ,  $\epsilon = .72$ ,  $p = .13$ ). Indeed,  
548 Sadness elicited a stronger activity than Fear and Happiness ( $p = .01$  and  $p = .001$   
549 respectively with a Bonferroni correction for multiple comparisons).

550

### 551 3.2.3. Responses to facial expression changes at the individual level

552 All individual participants showed significant responses for each of the 6  
553 expression changes presented in upright faces, either in the left, the right or both left  
554 and right ROI (Z-score  $> 1.96$ , i.e.,  $p < .05$ ) (See Fig. 4). Moreover, *t*-tests were  
555 performed at individual level on the baseline-corrected amplitude data to examine the  
556 interhemispheric differences for each expression (see Fig. 4). In a large number of  
557 participants, larger responses were observed in right than in left hemisphere,

558 especially for Disgust (4 participants against 2, and 11 had activation in both  
 559 hemisphere), Fear (7 against 2, and 8 with no differences), Happiness (5 against 2,  
 560 and 10 with no differences) and Anger (7 against 1, 9 with no differences). In return,  
 561 larger responses were observed in the left hemisphere for Surprise (in 5 participants  
 562 against 4 in the right hemisphere, 8 with no differences) and Sadness (6 against 2, 9  
 563 with no differences).



564  
 565 **Fig. 4. Individual responses to emotional expression changes. A. Hemispheric**  
 566 **lateralization at individual level based on summed baseline-corrected amplitude for each**  
 567 **expression change (dark blue indicated a higher amplitude in the right than in the left**  
 568 **hemisphere; dark green indicated a higher amplitude in the left than in the right hemisphere ( $p$**   
 569  **$< .05$ ); light color (blue or green) indicated a trend toward significance ( $.05 < p < .07$ ) and**  
 570 **orange indicated a significant response in both left and right ROI without interhemispheric**

571 difference). B. Example of individual responses to the expression-specific frequency for four  
572 subjects. Three-dimensions scalp topographies (in  $\mu\text{V}$ ) of the summed expression-specific  
573 frequency response (i.e. 1.2 Hz) and its significant harmonics (until 8F/5, i.e. 9.6 Hz, excluding  
574 the base rate at 6 Hz) for each facial expression. The color scale indicates the range from 0 to  
575 the maximum individually for each subject, the same scale is used for the distinct expression  
576 for each subject.

577

#### 578 3.2.4. Topographical analysis

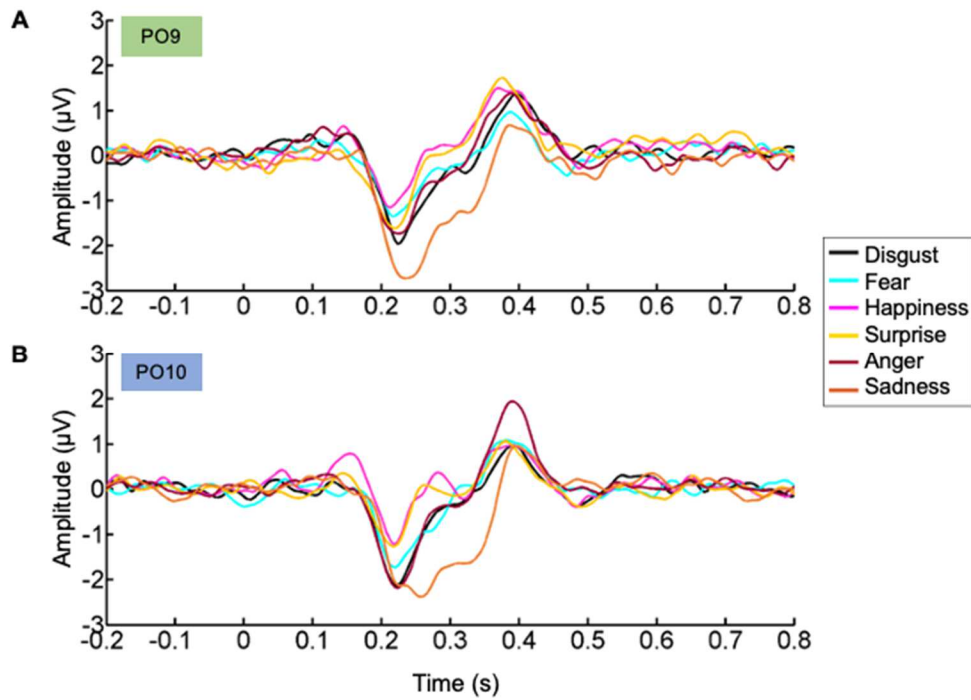
579 In order to evaluate the spatial differences characteristic to the expression  
580 changes of the six basic emotions on the 128 electrode sites, mass univariate  
581 analyses were performed. While no effect was found on any of the electrode sites in  
582 the inverted orientation (all  $p > .05$ ), a significant effect of *Expression* ( $p < .01$ ) was  
583 observed on 7 occipito-temporal electrodes in the upright orientation, namely 4  
584 electrodes in the left hemisphere (PO9, PO11, I1, POI1) and 3 in the medial region  
585 (POOz, Oz, Olz). Over the left occipito-temporal electrodes (PO9, PO11, I1, POI1),  
586 higher activities were recorded for Disgust and Sadness compared to Fear (all  $p <$   
587  $.027$ ), indicating a stronger left lateralization for the former expressions than for Fear,  
588 and reinforcing the left lateralization for Sadness expression as revealed by the  
589 conventional analysis. However, on the electrodes located on medio-posterior region  
590 (POOz, Oz, Olz), Happiness and Anger elicited higher responses compared to all  
591 other expressions (all  $p < .0268$ ), suggesting a more medial distribution for these  
592 expressions.

593

#### 594 3.2.5. Time-domain analyses

595 These analyses, by subtracting Upright *minus* Inverted faces, revealed the  
596 succession of two clear deflections in occipito-temporal (PO9/PO10) sites following  
597 the presentation of an emotional expression (see Fig. 5): a negativity peaking at  
598 around 235 msec and lastly, followed by a positivity at around 397 msec (note that  
599 the sinusoidal presentation leads to a slight delay before the image is visible on the  
600 screen). Time-point analyses ( $p < .05$ , for at least 5 consecutive points,  
601 approximately 20 msec) on differential waveforms for each expression change  
602 showed significances during the time window from 189 msec to 346 msec over  
603 bilateral occipito-temporal sites for all the expressions, except for Surprise over the  
604 right occipito-temporal sites and Happiness in both hemispheres. Finally, significant  
605 differences appeared between 349 and 431 msec over bilateral occipito-temporal

606 sites for all the expressions, except for Surprise and Disgust for which the responses  
607 appeared only on the left hemisphere and Sadness for which responses did not  
608 appear either in left or in the right hemisphere (see Table 2).



609  
610 **Fig. 5. Temporal dynamics of the brief expression changes detection. The differential**  
611 **responses between upright and inverted faces are shown independently for each emotional**  
612 **expression over two occipito-temporal channels A. in the left hemisphere (PO9) and B. in the**  
613 **contralateral hemisphere (PO10). Data are displayed for a segment of 1 second locked to the**  
614 **presentation of the emotional expression, and these EEG data are shown with the signals at**  
615 **6Hz and its harmonics filtered out.**  
616

617  
618

PO9	First time window		Second time window	
	Start	End	Start	End
Disgust	208	263	380	415
Fear	204	240	388	403
Happin ess			349	415
Surpris e	189	231	361	403
Anger	204	286	361	431
Sadnes s	208	333		

619

PO10	First time window		Second time window	
	Start	End	Start	End
Disgust	208	255		
Fear	212	271	376	423
Happin ess			369	415
Surpris e				
Anger	208	259	369	411
Sadnes s	224	345		

620 **Table 2.** Time course (in msec) of the detection of emotional expression changes. Time  
621 points at which differential waveforms (upright *minus* inverted) for each emotional expression  
622 differed significantly ( $p < .05$ ) over left (PO9) and right (PO10) occipito-temporal channels.  
623

#### 624 4. Discussion

625 With FPVS-EEG, we provide evidence of the human brain's ability to reliably  
626 detect changes from neutral faces to briefly presented facial emotions with highly  
627 heterogeneous natural images, i.e. varying in terms of background, head orientation,  
628 identity, age, lighting condition, ethnical origin, etc. Whole scalp analysis showed



629 activities mainly over posterior regions. In particular, emotional face detection elicited  
630 activity over occipito-temporal sites, with distinct hemispheric lateralization and  
631 cortical topographies according to the specific expression. Analysis centered on  
632 posterior ROI highlighted higher activity for the expression of Sadness as compared  
633 to Fear and Happiness. Taking into account interhemispheric differences, Sadness  
634 and Surprise elicited larger responses over the left hemisphere whereas Fear elicited  
635 a larger response over the right hemisphere. The other emotions (Disgust,  
636 Happiness, Anger) activated both hemispheres to the same extent. Finally, brain  
637 topographical analysis underlined stronger responses over medio-posterior regions  
638 for Happiness and Anger, while Disgust and Sadness recruited the left lateral  
639 occipito-temporal regions to a larger extent than Fear.

640

#### 641 **4.1. Robust electrophysiological marker of emotional face categorization**

642 The present study highlighted the capacity of the brain to automatically  
643 categorize facial expressions from visual stimuli embedded in a natural environment.  
644 Faces were presented rapidly (with a 166 msec SOA) in a continuous train of  
645 stimulation and despite the brief appearance of expressive faces every five faces (i.e.  
646 at a 1.2 Hz rate), highly significant neural responses were observed at that frequency  
647 of interest in the EEG spectrum. Moreover, despite the great variability of the images,  
648 these responses were significant not only at the group level but also at the individual  
649 level, thus underlining the robustness of the responses observed with this approach.

650 Several sources of evidence suggest that the recorded neural response to  
651 expression changes reflect high-level processes. Indeed, even if picture size did not  
652 vary across images (unlike in the previous FPVS-EEG studies measuring  
653 discrimination of facial expression, e.g., Dzhelyova et al., 2017; Leleu et al., 2018),  
654 size and spatial location of the faces in the images were highly variable across  
655 stimuli, so that the changes of expression could not be captured by simple local (i.e.  
656 pixelwise) changes of the stimuli. Most importantly, all stimuli varied considerably in  
657 terms of their background, head orientation, sex, identity, age, etc. so that the  
658 differential response occurring at 1.2 Hz (and expressed as a sum of harmonics of  
659 that frequency) could not be attributed to the same systematic differences with the  
660 neutral faces. Hence, the expression-specific response (i.e., 1.2 Hz) was massively  
661 and significantly reduced for inverted faces, showing that this response largely  
662 reflects high-level processes. Moreover, the probability of appearance of each image

663 (neutral or expressive faces) in each stimulation sequence was strictly equal, and the  
664 fast rate of stimulation together with the high variability of images in such paradigms  
665 prevent participants to temporally track the appearance of expression changes (i.e.,  
666 the “oddball” response is not due to temporal predictability, see Quek & Rossion,  
667 2017). Yet, one acknowledged limitation of our study is the small number of pictures  
668 used for each emotional expression, both in order to equalize the repetition of each  
669 image and because of to the difficulty of finding clear natural images of expressive  
670 faces.

671 Overall, all these elements indicate that the neural responses to the detection  
672 of expression changes are related to high-level processes linked to emotion  
673 processing rather than to low-level processes linked to specific visual characteristics  
674 of the images.

675

#### 676 **4.2. Human brain detection of facial expression according to emotion**

677 When all basic emotional expressions are evaluated, Fear generally elicits the  
678 largest neural response (Batty & Taylor, 2003; Poncet et al., 2019; Turano et al.,  
679 2017; but see Lynn & Salisbury, 2008), whereas the smaller response is reported for  
680 Sadness (Leleu et al., 2018). This is in line with behavioral evidence that Sadness is  
681 often confused with neutral expressions (Palermo & Coltheart, 2004; Tottenham et  
682 al., 2009). Moreover, previous frequency-tagging EEG research has revealed that the  
683 human brain’s activity increases with increasing intensity of the different type of  
684 emotion, with a 40 % threshold for all the expressions, except for sadness for which  
685 the detection intensity threshold was 60 % (Leleu et al., 2018) when prototypical  
686 expressions are presented. Here, in contrast to these observations, the largest  
687 activity over occipito-temporal sites was observed to Sadness, significantly stronger  
688 than for Fear and Happiness. This discrepancy with previous studies could be  
689 explained by the high variability of the images used here, contrasting with the  
690 majority of studies on emotional perception that used stereotypical and posed faces.  
691 For instance, the presence of tears and its important social meaning could amplify  
692 the differences of neural response between neutral and sad faces and, in our attempt  
693 to match the intensity of all expressions, we could have potentially selected more  
694 triggering sad expressions compared to prototypical images. More generally,  
695 previous behavioral and neuroimaging studies have shown that gaze direction  
696 (directed or averted; e.g. Adams et al., 2012; Conty, N’Diaye, Tijus & George, 2007;

697 Milders, Hietanen, Leppänen & Braun, 2011; Sander, Grandjean, Kaiser, Wehrle &  
698 Scherer, 2007), head orientation (e.g. Hess, Adams & Kleck, 2007; Sauer, Mothes-  
699 Lasch, Miltner & Straube, 2014), ethnical origin (e.g. Beaupré & Hess, 2006; Jack et  
700 al., 2009; Krämer et al., 2014; see Nelson & Russel, 2013 for a review) but also  
701 emotional scenes in background (e.g. Righart & de Gelder, 2008a, 2008b; Xu et al.,  
702 2017) could influence the recognition of emotional expressions and underlying neural  
703 activities. More specifically, regarding contextual influence, when emotional faces are  
704 more subtle, the context would facilitate their recognition (Bublitzki et al., 2020; Xiao  
705 et al., 2016).

706 We also observed a different lateralization of brain responses depending on  
707 facial expressions, with stronger activity over left than right occipito-temporal sites for  
708 Sadness and Surprise and the opposite for Fear. Hemispheric lateralization  
709 differences have often been explained as a result of different processing strategies,  
710 with the right hemisphere being more dedicated in holistic processing of the face  
711 (Caharel et al., 2013; Hillger & Koenig, 1991; Jacques & Rossion, 2009; Rossion et  
712 al., 2011; Sergent, 1988; Sergent et al., 1992) while the left hemisphere would be  
713 relatively more involved in analytic processing (Hillger & Koenig, 1991; Sergent,  
714 1982). These observations have also been reported more recently for emotional  
715 expression perception. For example, Calvo and Beltrán (2014) reported distinct  
716 amplitudes of ERP components between emotional expressions when the whole face  
717 was presented in the right hemisphere, while higher responses were observed in the  
718 left hemisphere when presenting isolated facial features (e.g., smiling mouth). Using  
719 eye tracking, Calvo and Nummenmaa (2008) found that participants focus  
720 preferentially on critical regions to categorize a given expression, for example on the  
721 mouth for Happiness and Disgust and on the eye region for Fear, Sadness and  
722 Anger (Bombari et al., 2013; Wegrzyn, Vogt, Kireclioglu, Schneider & Kissler, 2017).  
723 Thus, our results might suggest that the saliency of the eye region, and possibly the  
724 tears, in sad faces leads to an increase in part-based processing subtended  
725 preferentially by the left hemisphere, whereas the detection of Fear would be  
726 relatively more holistic, preferentially subtended by the right hemisphere. This latter  
727 result is supported by increased inversion effects for Fearful faces compared to  
728 Happiness and Disgust (Dzhelyova et al., 2017). This holistic processing for Fear  
729 could explain the reduced brain activity observed here, as this emotion could be  
730 discriminated at a glance without checking every single part of the face thus leading

731 to a lesser attentional cost. In the same vein, the higher activity for a face expressing  
732 Sadness could be explained by a higher attentional recruitment to be processed part  
733 by part, especially driven by eye-regions (Bombari et al., 2013; Wegrzyn et al., 2017).  
734 Despite strong evidence of the preferential involvement of holistic processing, it has  
735 been shown that emotional faces are recognized above chance level when the  
736 stimuli are scrambled, inverted or blurred, thus suggesting that both processes can  
737 be used (Bombari et al., 2013). In our study, the lack of difference of interhemispheric  
738 activation for Disgust, Anger and Happiness suggests that the detection of these  
739 expressions would be based on a combination of both holistic and feature-based  
740 processing. These latter results regarding Anger and Happiness corroborate previous  
741 findings highlighting the implication of these two modes of processing for these  
742 expressions (Meaux & Vuilleumier, 2016).

743 Finally, although Surprise has been less frequently studied (Leleu et al., 2018;  
744 Lynn & Salbury, 2009; Poncet et al., 2019), it was previously assumed that diagnostic  
745 features are not clear for this facial expression (Calvo & Beltrán, 2014; Calvo,  
746 Fernández-Martín, Gutiérrez-García, & Lundqvist, 2018). For example, Smith,  
747 Cottrell, Gosselin & Schyns (2005) emphasized the involvement of the mouth in their  
748 response classification technique, whereas Guo (2012) emphasized on the  
749 importance of the eye region for the recognition of Surprised faces. However, the  
750 involvement of the left hemisphere during the processing of this facial expression in  
751 our study using natural and highly variable images suggests that it could be  
752 processed rather part by part than holistically, contrary to previous research  
753 suggesting a holistic processing by using posed and decontextualized faces (Calvo &  
754 Beltrán, 2014). Future studies will be necessary to disentangle the respective  
755 implication of holistic and feature-based processing depending on the type of  
756 emotion as well as the impact of contextual and dynamic aspects in expression  
757 processing.

758

#### 759 **4.3. Differential spatial distributions depending on emotional expressions**

760 Although occipito-temporal activity was prominent for each of the 6  
761 expressions, our study highlighted two distinct neural signatures according to the  
762 expression. More specifically, Happiness and Anger produced larger responses over  
763 medio-occipital region compared to other expressions, while Disgust and Sadness  
764 produced larger over the left lateral occipito-temporal region than Fear. Distinct

765 spatial occipito-temporal distributions were also previously found by means of a  
766 similar FPVS-EEG paradigm (Dzhelyova et al., 2017; Leleu et al., 2018). Dzhelyova  
767 et al. (2017) observed more dorsal occipito-temporal distribution for Happiness and  
768 more ventral occipito-temporal distribution for Fear and Disgust expression. These  
769 authors interpreted this distinct distribution in terms of regions involved in avoidance  
770 or approach-related expressions (see Elliot & Covington, 2001 for a review). These  
771 two motivational systems would be underpinned by distinct neural substrates  
772 (Pizzagalli, Sherwood, Henriques & Davidson, 2005). In line with this interpretation,  
773 our observations pointed out more medio-occipital distributions for Anger and  
774 Happiness, both being associated with approach-related expression (Carver &  
775 Harmon-Jones, 2009; Davidson, 1992). In contrast, the other expressions, Disgust,  
776 Surprise and Sadness (except Fear), recruiting more lateral occipito-temporal  
777 regions, are generally associated with avoidance (Lee & Lang, 2009).

778

#### 779 **4.4. Time course of facial expression discrimination**

780 Our analyses revealed two time-domain responses during which expressive  
781 faces were discriminated from neutral faces, with specific patterns according to the  
782 emotional expressions. A first temporal window appeared early between 189 and 346  
783 msec and a second temporal window occurred later between 349 and 431 msec over  
784 occipito-temporal regions. Our results thus highlight a rapid discrimination of  
785 emotional faces among neutral ones for all expressions as soon as the first time  
786 window, except for Happiness for which this discrimination only appears later, during  
787 the second time window. Even if a strict comparison between the time components  
788 observed during FPVS and ERPs obtained during standard stimulation cannot be  
789 drawn, the time windows identified here are similar to the modulation of ERP  
790 components by facial expressions (e.g., N170: Balconi & Mazza, 2009; Batty &  
791 Taylor, 2003; Eimer, Holmes & McGlone, 2003; Meaux, Roux & Batty, 2014).

792 Specifically, we observed a large (189-346 msec) window during which a  
793 bilateral negativity occurred over occipito-temporal sites for all expressions (except  
794 Happiness in both hemisphere and Surprise in the right hemisphere). This time  
795 window could be put in parallel with the well-known N170 component, a negative  
796 component, peaking between 140 and 200 following stimulus onset. This face-  
797 sensitive component (see Rossion & Jacques, 2008 for review), associated with  
798 structural encoding of faces (Bentin, Allison, Puce, Perez & McCarthy, 1996), has

799 been shown to be modulated by facial expression using static (e.g. Batty & Taylor,  
800 2003; Caharel et al., 2007; DaSilva, Crager & Puce, 2016; Leppänen, Kauppinen,  
801 Peltola & Hietanen, 2007) and dynamic (ERPs: Miyoshi et al., 2004; MEG: Sato,  
802 Kochiyama & Uono, 2015) presentations. Notably, its amplitude increases for  
803 negative expressions compared to positive ones (e.g. Batty & Taylor, 2003; Caharel  
804 et al., 2007; Turano et al., 2017; see Hinojosa, Mercado & Carretié, 2015 for a meta-  
805 analysis). Qualitatively, we also observed in the present study larger waveform  
806 amplitudes for negative emotions, especially for Sadness compared to Happiness  
807 and Surprise. Recently, a study highlighted the sensitivity of the N170 to the eye-  
808 regions by combining eye movements analysis and EEG recording when participants  
809 visualized emotional faces (Neath-Tavares & Itier, 2016). Thus, a possible  
810 explanation for the larger amplitude observed for Sadness could be that the  
811 processing of this emotion is relatively more dependent on the eye regions, as  
812 previously mentioned (Bombari et al., 2013; Wegrzyn et al., 2017).

813 Altogether, we observed clear categorization responses of emotional  
814 expression appearing as soon as early perceptual stages of face processing.

815

## 816 **5. Conclusions**

817 To conclude, the present study provides objective evidence for robust rapid and  
818 automatic facial expression categorization processes in the human brain from highly  
819 variable natural images. Specifically, our findings highlighted that this ability of the  
820 human brain to detect facial emotions can be generalized across changes of identity,  
821 viewpoint, sex, ethnic origin, but also across the context of the image (natural  
822 environments). This effect is extremely robust since it was observed for each change  
823 of expression in every individual tested, emphasizing the high sensitivity of the FPVS-  
824 EEG approach.

825

### 826 **Data and code availability**

827 The study data is available at <https://data.4tu.nl> .

828 The EEG data were analyzed using the open source Letswave software package  
829 (<https://github.com/NOCIONS/Letswave5>), running in MATLAB R2013a (MathWorks,  
830 USA).

831 All face stimuli used in the experiment were collected from the Internet. The  
832 identity of the copyright holders was unknown, thus preventing us from making the  
833 face stimuli publicly available or sharing them.

834 EEG data, behavioral data and data analysis steps of the study are available at  
835 <https://osf.io/tkrha/>.

836 The experimental design was implemented using custom software written in Java.  
837 The code is available at <https://osf.io/tkrha/>.

838 No part of the study procedures and analyses was pre-registered prior to the  
839 research being conducted.

840

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846

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