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► **To cite this version:**

Fabrice Damon, Arnaud Leleu, Diane Rekow, Fanny Poncet, Jean Yves Baudouin. Expertise for conspecific face individuation in the human brain. *NeuroImage*, 2020, 204, pp.116218. 10.1016/j.neuroimage.2019.116218 . hal-02297307

HAL Id: hal-02297307

<https://hal.science/hal-02297307>

Submitted on 20 Jul 2022

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Expertise for conspecific face individuation in the human brain

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Acknowledgments:

This work was supported by the French “Investissements d’Avenir” program, project ISITE-BFC (contract ANR-15-IDEX-0003), the “Conseil Régional Bourgogne Franche-Comté”, and the FEDER (European Funding for Regional Economic Development), and a PhD scholarship from the French MESR to F.P. The authors are grateful to the people who participated in the study, to Renaud Brochard for EEG funding, and to Véronique Boulanger for recruitment.

Expertise for conspecific face individuation in the human brain

Abstract

Humans exhibit a marked specialization to process the most experienced facial morphologies. In particular, nonhuman primate faces are poorly discriminated compared to human faces in behavioral tasks. So far however, a clear and consistent marker that quantifies our expertise in human over monkey face discrimination directly from brain activity is lacking. Here, using scalp electroencephalography (EEG), we isolate a direct signature of individuation abilities for human and nonhuman (i.e., macaque faces) primate faces. Human or monkey faces were rapidly presented at a base rate of 12 Hz in upright or inverted orientations while participants performed an orthogonal behavioral task. In each stimulation sequence, eight face images of one individual were used as base stimuli, while images of other individuals were briefly introduced every 9th stimulus to quantify an identity-change response at 1.33 Hz and harmonics (i.e., integer multiples) in the EEG frequency spectrum. The brain response to upright human faces was twice as large as to monkey faces, and reduced following picture-plane inversion for human faces only. This reflects the disruption of high-level face identity discrimination developed for the canonical upright human face. No difference was observed between upright monkey faces and inverted human faces, suggesting non-expert visual processes for those two face formats associated with little experience. In addition, the size of the inversion effect for human, but not monkey faces, was predictive of the expertise effect (i.e., difference between upright human and monkey faces) at the individual level. This result suggests a selective ability to discriminate human faces that does not contribute to the individuation of other unexperienced face morphologies such as monkey faces. Overall, these findings indicate that human expertise for conspecific face discrimination can be isolated and quantified in individual human brains.

Keywords: FPVS-EEG; Face individuation; Expertise; Visual discrimination; Human; Monkey

Data and Code Availability:

The authors confirm that the data supporting the findings of this study are available within the article or its supplementary materials. Details of raw data that support the findings of this study are available from the corresponding author, F.D., upon reasonable request.

Expertise for conspecific face individuation in the human brain

Introduction

Visual discrimination of face identity is a fundamental and complex function of the human brain with critical implications for social interactions. Face individuation is readily achieved with apparent simplicity and automaticity despite subtle physical differences between individual faces and widely variable exposure conditions (e.g., viewing angle, lighting, facial expression). Such a high-level perceptual ability led to the view that humans are natural experts at individuating faces due to extensive experience with this visual category (e.g., Carey, 1992; for a recent debate see Rossion, 2018; Sunday & Gauthier, 2018; Young & Burton, 2018a, 2018b, 2018c). Accordingly, humans exhibit a marked specialization to process the most experienced faces over less experienced ones, such as same-race over other-race faces (i.e., "other-race effect", for reviews see Meissner & Brigham, 2001; Rossion & Michel, 2011) or same-age over other-age faces (i.e., "other-age effect", Kuefner, Macchi Cassia, Picozzi, & Bricolo, 2008; for a review see, Rhodes & Anastasi, 2012).

As a general account of visual expertise for a certain class of faces, numerous studies have documented how experience tunes the face perception system towards conspecific over other-species face morphologies (Dufour, Coleman, Campbell, Petit, & Pascalis, 2004; Dufour, Pascalis, & Petit, 2006; Pascalis & Bachevalier, 1998; Pascalis, de Haan, & Nelson, 2002; Simpson, Jakobsen, Damon, Suomi, & Ferrari, 2017; Sugita, 2008), the so-called "other-species effect" (OSE, Scott & Fava, 2013). This high-level perceptual expertise has a long-standing developmental history that can be traced back into early infancy (i.e., the "perceptual narrowing" mechanism, for review see Maurer & Werker, 2014), and extends to nonhuman primates (Simpson, Jakobsen, Damon, Suomi, & Ferrari, 2017; Sugita, 2008). In particular, despite commonalities with human faces due to phylogenetical proximity (Balas & Stevenson, 2013; Taubert, 2009), nonhuman primate faces are poorly discriminated by humans in both explicit (e.g., face matching or search tasks, Dufour & Petit, 2010; Scott, Shannon, & Nelson, 2005; Wu et al., 2015) and implicit (i.e., visual paired comparison, Dufour et al., 2006; Pascalis & Bachevalier, 1998; Pascalis et al., 2002) behavioral tasks. Subtle differences in the arrangement of facial features are also better detected in human than monkey faces (e.g., Dahl, Logothetis, Bülthoff, & Wallraven, 2010, 2011; Dahl, Rasch, & Chen, 2014; Dahl, Wallraven, Bülthoff, & Logothetis, 2009; Mondloch, Maurer, & Ahola, 2006). Similarly, while picture-plane inversion strongly disrupts human face individuation (the well-know "face inversion effect", Yin, 1969, for reviews see Rakover, 2013; Rossion,

68 2008; Valentine, 1988) indexing greater experience with the canonical upright face format
69 (Albonico, Furubacke, Barton, & Oruc, 2018; Carey & Diamond, 1977; Diamond & Carey,
70 1986; Rossion & Gauthier, 2002; Valentine, 1988; White, Phillips, Hahn, Hill, & O'Toole,
71 2015), it affects the discrimination of nonhuman primate faces to a lesser extent (Dufour et
72 al., 2004; Taubert, 2009).

73 Studies using scalp electroencephalography (EEG) are ideally suited to characterize a
74 direct neural signature of this well-established behavioral advantage in processing human over
75 nonhuman primate faces. The N170, peaking at around 150-170 ms after stimulus onset over
76 the occipito-temporal cortex (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bötzel,
77 Schulze, & Stodieck, 1995; Carmel & Bentin, 2002; Rossion et al., 2000), is the earliest
78 event-related potential (ERP) component showing strong sensitivity (i.e., larger amplitude) to
79 faces over non-face objects (for reviews see Eimer, 2011; Rossion, 2014; Rossion & Jacques,
80 2011). The N170 elicited by nonhuman primate faces is delayed (Balas & Stevenson, 2013;
81 Carmel & Bentin, 2002; de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson,
82 2003; Itier, Van Roon, & Alain, 2011; Rousselet, Mace, & Fabre-Thorpe, 2004; Wiese, Stahl,
83 & Schweinberger, 2009) and of larger amplitude (Balas & Stevenson, 2013; de Haan et al.,
84 2002; Itier et al., 2011; Schweinberger, Huddy, & Burton, 2004; Scott et al., 2005) compared
85 to human faces. However, the latter effect seems less robust (Rossion, Curran, & Gauthier,
86 2002) as some studies either failed to find significant amplitude differences (Carmel &
87 Bentin, 2002; Rousselet et al., 2004; Wiese et al., 2009), or even reported a decrease in
88 amplitude (Gajewski & Stoerig, 2011). The difference between the N170 evoked by human
89 and monkey faces strikingly mirrors the N170 inversion effect for human faces with a delayed
90 and sometimes enhanced peak response to upside-down faces (e.g., Caharel, Fiori, Bernard,
91 Lalonde, & Rebaï, 2006; de Haan et al., 2002; Eimer, 2002; Marzi & Viggiano, 2007; Rossion
92 et al., 1999, 2000; Rossion & Gauthier, 2002; Sadeh & Yovel, 2010). Therefore, picture-plane
93 inversion modulates the N170 more strongly for human than nonhuman primate faces (Itier et
94 al., 2011; Rousselet et al., 2004; Wiese et al., 2009), suggesting that monkey faces recruit
95 non-expert visual processes in both orientations.

96 However, it is worth noting that the aforementioned ERP studies simply contrasted the
97 sudden onset of a face stimulus (either human or nonhuman) with a no-stimulus baseline, and
98 thus did not isolate face individuation processes in the brain. A few ERP studies used
99 adaptation/repetition paradigms to tap the visual discrimination of both human and nonhuman
100 primate faces, but they did not find a repetition effect on the N170/M170 for either category

101 (Schweinberger et al., 2004; Schweinberger, Kaufmann, Moratti, Keil, & Burton, 2007). In
102 contrast, these studies observed an increased amplitude of the subsequent N250/M250
103 component with face repetition, which was either similar for the two categories
104 (Schweinberger et al., 2007), or slightly larger for human faces (Schweinberger et al., 2004).
105 In addition, these studies did not use different images of the same individual face and cannot
106 exclude a low-level image-based account of the repetition effect. So far, EEG studies thus did
107 not provide a clear and consistent marker that quantifies our expertise in human over monkey
108 face individuation directly from brain activity.

109 Here, we tackle this issue and isolate a direct signature of greater individuation ability
110 for human over monkey faces in the human brain using fast periodic visual stimulation
111 (FPVS) coupled with EEG frequency-tagging. In previous studies, FPVS-EEG has
112 successfully characterized a neural marker of human face discrimination (Dzhelyova &
113 Rossion, 2014b, 2014a; Liu-Shuang, Norcia, & Rossion, 2014) whose amplitude is
114 substantially reduced by picture-plane inversion (Liu-Shuang et al., 2014). Moreover,
115 individual identity-change responses obtained with this approach are associated with explicit
116 behavioral performance in face discrimination tests (Xu, Liu-Shuang, Rossion, & Tanaka,
117 2017; for a relationship between eye movements and neural face discrimination see also
118 Stacchi, Ramon, Lao, & Caldara, 2019), and relate to face individuation impairment in
119 acquired prosopagnosia (Gao, Vuong, & Rossion, 2018; Liu-Shuang, Torfs, & Rossion,
120 2016). The FPVS-EEG approach is thus ideally suited to provide a direct and implicit neural
121 signature of face individuation abilities.

122 In the present study, human or nonhuman (i.e., macaques faces, *macaca mulata*)
123 primate faces were rapidly presented at a base rate of 12 Hz (i.e., 12 images per second, ≈ 83
124 ms per image). Each stimulation sequence consisted in the repeated presentation of 8 images
125 of the same individual (e.g., individual A, see Figure 1), followed by the brief appearance of a
126 different individual from the same face category (i.e., human or monkey) every 9th cycle (i.e.,
127 at $12/9 = 1.33$ Hz, different individuals at each identity change, e.g., individuals B, C, etc.).
128 To avoid low-level image-based adaptation to the repeated individual face, images varied at
129 each stimulation cycle with a change of head pose. This manipulation constrains the visual
130 system to extract face identity across images, excluding face discrimination based on low-
131 level cues. Two brain responses were thus dissociated within a single stimulation sequence.
132 The base response recorded at 12 Hz and harmonics (i.e., integer multiples) reflects the rapid
133 processing of every cue changing 12 times per second (e.g., local contrast, head pose). The

134 identity-change response measured at 1.33 Hz and harmonics is a direct marker of individual
135 face discrimination without subtracting out any control condition response (i.e. a direct
136 *differential* response to the perceived change of identity). In addition, faces were presented
137 upright or upside-down in different stimulation sequences to isolate the expert face
138 individuation processes developed for the familiar upright orientation. Finally, participants
139 performed a non-periodic orthogonal task (i.e., cross detection) that eliminates the
140 contribution of decisional/motor processes in the brain responses of interest. Hence, FPVS-
141 EEG is a unique approach to provide a quantified electrophysiological measure of high-level
142 individual face discrimination with objectivity (at the exact predefined frequencies of
143 stimulation) and high signal-to-noise ratio (SNR, i.e., the brain responses are captured in a
144 few frequency bins within the EEG amplitude spectrum) in every participant (Liu-Shuang,
145 Norcia, & Rossion, 2014). We therefore characterize the expert perceptual processes
146 developed by human participants for the rapid (i.e., at a glance) and automatic individuation
147 of human over monkey faces.

148 **Material and methods**

149 **Participants**

150 We tested twenty-eight participants (15 females, 1 left-handed; $M_{\text{age}} = 27.41$ years, SD
151 $= 6.93$ years, range: 20–44 years). Participants had no specific history of being familiar with
152 rhesus monkey faces. All reported normal or corrected-to-normal visual acuity, and none
153 reported any history of neurological or psychiatric illness. They provided written informed
154 consent prior to beginning the experiment and were financially compensated for their
155 participation. Testing was conducted in accordance with the Declaration of Helsinki.

156 **Stimuli**

157 We used 72 male Caucasian faces and 72 Japanese macaque faces. Japanese macaques
158 faces came from the PrimFace database (<http://visiome.neuroinf.jp/primface>), and human
159 faces came from the PUT Face Database (<http://biometrics.put.poznan.pl/put-face-database>,
160 Kasinski, Florek, & Schmidt, 2008). Images were cropped to discard background and body
161 information, and converted to greyscale images to neutralize chromatic differences between
162 the two species. For both species, images depicted nine different individuals, each represented
163 in eight different images with variable head poses (i.e., yaw: $\pm 40^\circ$, pitch: $\pm 40^\circ$). The final set
164 of stimuli was thus composed of 144 pictures, 8 for each individual face (9 individuals, 2
165 species). Pictures were set to a size of 6.5×8.5 cm for human faces, and 7.3×7.5 cm for

166 macaque faces (i.e., $6.5 \times 8.5^\circ$, and $7.3 \times 7.5^\circ$ of visual angle at a distance of 57 cm,
167 respectively), thus human and macaques faces covered a similar surface area (i.e., $\approx 55 \text{ cm}^2$).

168 To ensure that faces from one or the other category were not physically more variable,
169 we assessed within-category similarity using the complex wavelet structural similarity index
170 (CW-SSIM, Sampat, Wang, Gupta, Bovik, & Markey, 2009) implemented on Matlab 2017
171 (MathWorks, USA). CW-SSIM is a computational measure of image similarity that
172 quantifies the difference between images while being robust to small rotations and
173 translations (ranging from 0 to 1, 1 reflecting perfect similarity). Note that equating face
174 discriminability within each stimulus set based on human assessments would have been
175 strongly biased since human ratings would have reflected differential expertise for human and
176 monkey faces. For the two categories, we computed the similarity index for each individual
177 face compared to all the other faces in the set. For example, for the human face1, we
178 computed the index for the 8 pictures corresponding to this individual with the 64 remaining
179 pictures of the set of human faces (i.e., 8 different pictures per individual \times 8 different
180 individuals). The similarity index was not significantly different between the two categories
181 ($M_{Human} = 0.763$, $SD = 0.089$, $M_{Monkey} = 0.766$, $SD = 0.097$, $t[9214] = -1.06$, $p = .29$, Cohen's d
182 $= 0.02$, 95 % $CI = [-0.0059; 0.0017]$, see supplementary material for raw values), indicating
183 that the two sets of faces were of similar physical variability.

184 Procedure

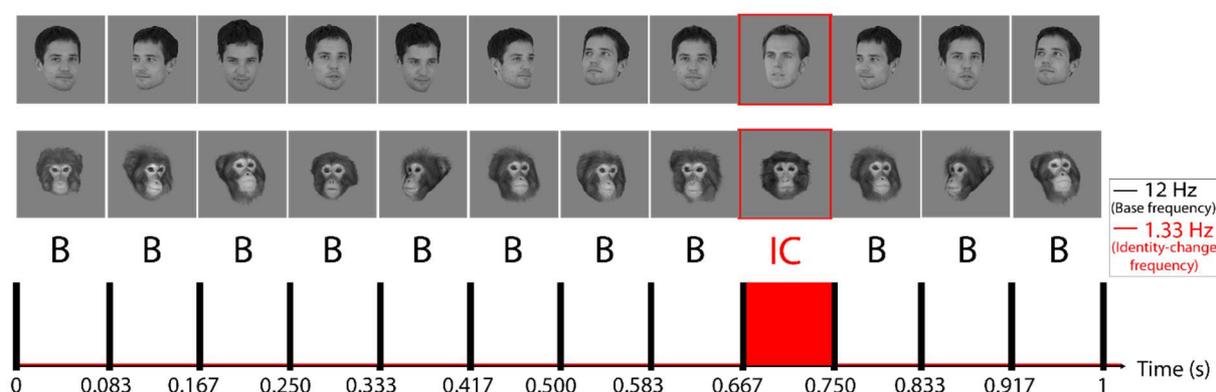
185 Stimuli were presented on a 24-inch LED screen with a 60 Hz refresh rate and a
186 resolution of 1920×1080 pixels. They were presented on a mid-level grey background (i.e.,
187 $128/255$ in greyscale) at a fast base rate of 12 Hz using custom software written in Java. At
188 this rate, each stimulus lasts ≈ 83 ms (i.e., $1 \text{ s}/12$). In each stimulation sequence, the eight face
189 images of one individual were used as base stimuli (B). Images of other individuals were
190 introduced every 9th stimulus, thus corresponding to an identity-change (IC) frequency of $12/9$
191 $= 1.333$ Hz (i.e., ≈ 750 ms between two different identities, see Figure 1). Schematically, one
192 second of stimulation sequence is schemed BBBBBOBBB (Figure 1). Base stimuli were
193 randomly presented with the condition that no repetition of images occurred between two IC
194 presentations. IC stimuli were randomly drawn from the pool of 64 remaining faces (i.e., for
195 each species: 8 images of the 8 individuals), with no repetition.

196 Since our goal was to reveal expertise for conspecifics face individuation under tight
197 temporal constraints, we used a fast 12-Hz rate of image presentation. Previous studies have
198 shown that the visual system can discriminate human faces vs. non-face objects (Or, Retter, &

199 Rossion, 2019; Retter & Rossion, 2016a) and expressive vs. neutral faces (Dzhelyova,
 200 Jacques, & Rossion, 2017) at such a rapid presentation rate, or even at higher rates (e.g., 20
 201 Hz; Retter, Jiang, Webster, & Rossion, 2018). In addition, at stimulation frequencies above 10
 202 Hz, the base response is characterized with a typical medial occipital topography, peaking at
 203 Oz and without spreading to occipito-temporal regions (Alonso-Prieto, Belle, Liu-Shuang,
 204 Norcia, & Rossion, 2013; Dzhelyova et al., 2017). A base rate of 12 Hz thus allows for a
 205 better spatial dissociation between the base response and the identity-change response. For the
 206 latter response, the 1.33-Hz rate of identity change is similar or close to what was typically
 207 used in previous studies (e.g., 1.18Hz, Dzhelyova & Rossion, 2014; Liu-Shuang, Norcia, &
 208 Rossion, 2014; Liu-Shuang, Torfs, & Rossion, 2016; Rossion, Torfs, Jacques, & Liu-Shuang,
 209 2015, 1.2 Hz, Hagen & Tanaka, 2019; Xu, Liu-Shuang, Rossion, & Tanaka, 2017; 1.33 Hz,
 210 Or et al., 2019; Dzhelyova et al., 2017). This corresponds to a duration of 750 ms between
 211 each identity change, thus allowing enough time for a full response to unfold (i.e., ≈ 500 ms in
 212 duration, Dzhelyova & Rossion, 2014b).

213 Thirty-six conditions corresponding to the 9 identities \times 2 species (human and
 214 macaque) \times 2 orientations (upright and inverted) were tested within participants. Each
 215 sequence started with a pre-stimulation interval of a blank screen (1 s). It was followed by a
 216 1.417 s fade-in of increasing contrast modulation depth. Then, the stimulation at full contrast
 217 lasted 25.583 s, followed by a 0.667-s fade-out of decreasing contrast modulation depth, and a
 218 post-stimulation interval of 0.333 s of blank screen. Each species condition was repeated 18
 219 times (9 individual faces \times 2 orientations), resulting in 36 sequences of 28 s presented
 220 randomly across participants.

221



223 Figure 1. Schematic illustration of the experimental design. Pictures of individual human (top)
 224 or monkey (bottom) faces were presented at a base rate of 12 Hz (12 images/s, see Movies S1

225 and S2). The base stimuli (B) consisted of one identity presented from variable head poses,
226 with a change of identity introduced every 9th stimulus (IC, framed in red), at a rate of 12
227 Hz/9 = 1.33 Hz.

228 After electrode-cap placement, participants were seated in a light- and sound-isolated
229 cabin in front of the screen. Their head was held on a chinrest to be maintained at a distance
230 of 57 cm from the screen and to reduce movements. An orthogonal behavioral task was
231 designed leading participants to focus their attention on the center of the screen and to prevent
232 expertise effects related to selective attention (McGugin, Newton, Gore, & Gauthier, 2014).
233 During each sequence, participants were asked to detect brief (200 ms) appearances of a blue
234 fixation cross located at the center of the screen 6 random times within every 28-s sequence
235 by pressing the space bar with both index fingers. A minimum interval of 2 s between two
236 crosses appearances was introduced.

237

238 EEG recording

239 During the experiment, electroencephalogram (EEG) was continuously recorded from
240 a 64-channel BioSemi Active-Two amplifier system (BioSemi, The Netherlands) with
241 Ag/AgCl electrodes located according to the 10 – 10 classification system. During recording,
242 the Common Mode Sense (CMS) active electrode was used as reference and the Driven Right
243 Leg (DRL) passive electrode was used as ground. Electrode offset was reduced between ± 25
244 μ V for each electrode. EEG was digitalized at a sampling rate of 1024 Hz.

245

246 EEG analysis

247 Preprocessing

248 All EEG analyses were performed using Letswave 6 (<https://www.letswave.org/>)
249 running on Matlab 2017 (MathWorks, USA). Preprocessing and processing analyses steps
250 have been extensively documented in recent publications (Dzhelyova et al., 2017; Jacques,
251 Retter, & Rossion, 2016; Leleu et al., 2018; Retter & Rossion, 2016b, 2016a). EEG data were
252 bandpass filtered at 0.1–100 Hz using a butterworth filter (4th order) and downsampled to 200
253 Hz to reduce file size and computational load. The continuously recorded data were cropped
254 into 28-s segments for each stimulation sequence (fade-in + full contrast + fade-out + 0.333 s
255 after the fade-out), thus resulting in 36 EEG segments per participants (9 individual faces \times 2
256 orientations \times 2 species). We applied an independent component analysis (ICA) using the
257 runica algorithm (Bell & Sejnowski, 1995) to remove components corresponding to eye
258 blinks, and artifacts recorded over frontal and temporal electrodes. Artifact-prone channels

259 (i.e., with deflections exceeding $\pm 100 \mu\text{V}$ in at least two sequences) were replaced using
260 linear interpolation of the three neighboring clean channels (less than 4% of channels per
261 participant, Picton et al., 2000). EEG segments were then re-referenced to a common average
262 reference.

263

264 Frequency-domain analysis

265 EEG segments were cropped to remove the fade-in, resulting in 26.25-s segments
266 (25.583 s of full contrast and 0.667 s of fade-out, 5250 time bins in total, thirty-five 1.33-Hz
267 cycles). To reduce EEG activity non-phase-locked to the stimuli, the nine preprocessed data
268 segments obtained per condition were averaged in the time domain, thus resulting in a single
269 26.25-s segment per condition. A fast Fourier transform (FFT) was applied and amplitude
270 spectra were extracted with a high frequency resolution of $1/26.25 = 0.038 \text{ Hz}$.

271 We first calculated the signal-to-noise ratio (SNR) for each species and orientation on
272 the grand-averaged FFT spectra across participants. SNR was obtained by dividing the
273 amplitude at each frequency bin by the mean noise amplitude estimated from the 20
274 surrounding frequency bins (10 on each side, excluding the immediately adjacent bins and the
275 2 most extreme – minimum and maximum – bins; e.g., Leleu et al., 2018; Liu-Shuang et al.,
276 2014). SNR spectra were used for visualization and illustration purpose since responses at
277 high frequencies in the EEG are generally of low amplitude but may have a high SNR.

278 We next determined how many harmonics (i.e., integer multiples) were significant for
279 each brain response. After grand-averaging the FFT spectra across participants, electrodes and
280 conditions, Z-scores were computed as the difference between the amplitude at each
281 frequency bin and the mean noise amplitude (i.e., same estimation as for the SNR, see above)
282 divided by the standard deviation of the noise. Harmonics were considered significant until Z-
283 scores were no longer above 1.64 ($p < .05$, one-tailed, signal $>$ noise) for 2 consecutive
284 harmonics. The identity-change response was significant until the 10th harmonic (i.e., 13.33
285 Hz) and the base response was significant until the 4th harmonic (i.e., 48 Hz, harmonics were
286 not considered after the 50 Hz response elicited by AC power).

287 Z-scores were then calculated on FFT data summed until the 4th harmonic for the base
288 response, and until the 10th harmonic (excluding the 9th harmonic corresponding to the base
289 rate; i.e., 12 Hz) for the identity-change response. Summed amplitudes across harmonics were
290 used to quantify the overall response in the frequency-domain (Retter & Rossion, 2016a). In
291 average across species and orientation, all but one electrode (i.e., T7, $Z = 0.27$) over the scalp

292 reached significance for the base response (all Z s > 1.64 , greatest $Z = 25.98$ for Oz) while 48
293 electrodes reached significance for the identity-change response (greatest $Z = 7.15$ for P10).

294 Based on those channels identified for grand-averaged data pooled across conditions,
295 we determined different regions-of-interest (ROIs) to include in statistical analyses following
296 a data-driven approach used in previous studies (Leleu et al., 2018, 2019; Poncet, Baudouin,
297 Dzhelyova, Rossion, & Leleu, 2019). For each brain response, we scaled topographical
298 differences between electrodes on the global magnitude of the response (McCarthy & Wood,
299 1985). This normalization consists in dividing the amplitude at each channel by the square
300 root of the sum of squared amplitudes of these channels and allows identifying the electrodes
301 over which the response is largest irrespective of its global power. Then, Z -scores were
302 calculated on these normalized summed amplitudes, and only channels with significant
303 responses were included in ROIs. The electrodes included in each ROI differed according to
304 the response (base vs. identity-change). We composed three ROIs for the base response: left
305 and right posterior sites (LH: P1, P3, P5, P7, PO3, PO7, and RH: P2, P4, P6, P8, PO4, PO8,
306 respectively), and medial occipital sites (MO: Pz, POz, O1, O2, Oz, Iz). For the identity-
307 change response, significant channels were included in two ROIs: left and right posterior sites
308 (LH: P5, P7, P9, P03, P07, O1, and RH P6, P8, P10, PO4, PO8, O2, respectively).

309 Finally, both responses were quantified in a single value expressed in microvolt (μ V)
310 for statistical analyses. A baseline-correction was first applied to FFT amplitude spectra by
311 subtracting the mean amplitude of the noise (i.e., estimated from the 20 surrounding bins, see
312 above). Then, these baseline-corrected amplitudes (BCA) were summed across significant
313 harmonics. Summed BCA were calculated for every channel, condition, and participant.
314 Repeated-measures ANOVAs were then run on individual summed BCA data for the identity-
315 change response with species (Human, Macaque), orientation (Up, Inverted) and ROI (LH,
316 RH) as within-subject factors, and for base response with species (Human, Macaque),
317 orientation (Up, Inverted) and ROI (LH, RH, MO) as within-subject factors. We used the
318 Greenhouse-Geisser correction to adjust degrees of freedom whenever the assumption of
319 sphericity was violated. Significant effects were followed-up with post-hoc Tukey HSD
320 contrasts.

321 **Results**

322 Behavioral cross detection task

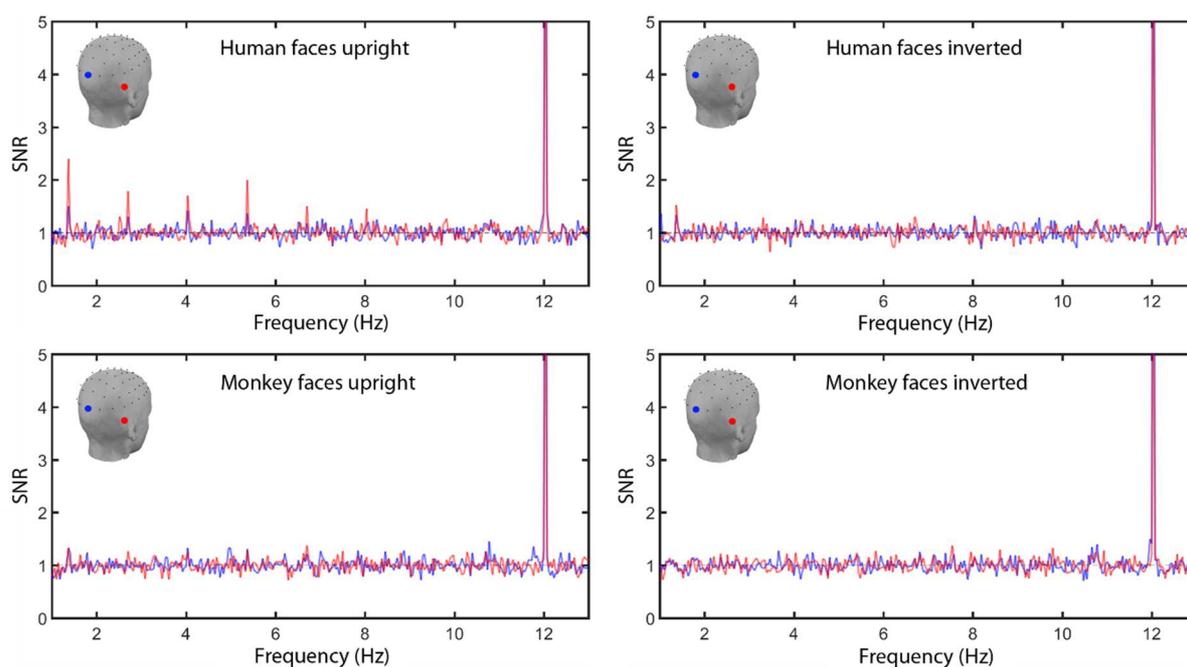
323 The cross detection task was well performed, with accuracy near ceiling in all
324 conditions (Table S1). This indicates that participants paid full attention to the screen during
325 the periodic stimulation. ANOVAs with Species and Orientation as within factors on

326 Accuracy and RT showed no differences between conditions ($M_{accuracy} = 99.07\%$, $SD_{accuracy} =$
 327 1.86% , $M_{RT} = 383$ ms, $SD_{RT} = 36$ ms, all $ps > .09$).

328 EEG data

329 SNR calculated on the FFT amplitude spectra (Figure 2) show that the 1.33-Hz brief
 330 changes of identity elicited clear brain responses at the same frequency and its harmonics for
 331 upright human faces (i.e., SNR between 1.5 and 2.5), whereas no responses were clearly
 332 visible for monkey faces in both orientations (i.e., $SNR \approx 1$). In comparison, the 12 Hz base
 333 rate elicited synchronized periodic EEG activities of high amplitudes, with the signal around 3
 334 to 18 times larger than the noise for all conditions.

335



336

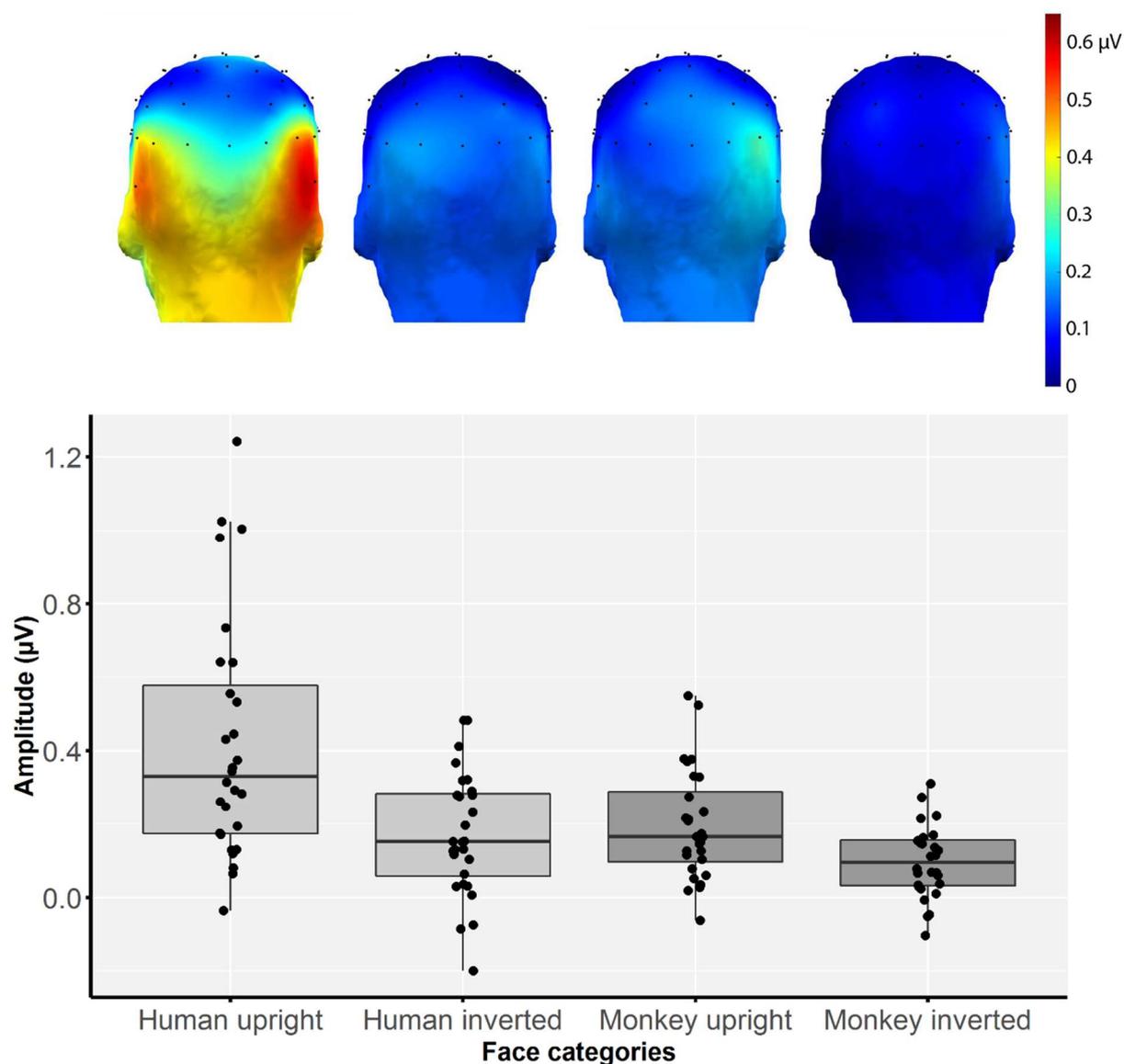
337 Figure 2. Grand-averaged FFT signal-to-noise ratio (SNR) spectra. SNR calculated on the
 338 grand-averaged FFT amplitude spectra for the different face categories (displayed from 1 to
 339 12 Hz) over the two channels showing the largest response at the identity-change (right
 340 occipito-temporal channel P10, red) and base (medial occipital channel Oz, blue) frequencies,
 341 respectively. Responses at the identity-change rate (1.33 Hz) and its harmonics (i.e., 2.66 Hz,
 342 4 Hz, etc.) are mostly visible for human upright faces, with greater SNR over P10 than Oz. In
 343 contrast, high SNR responses are clearly visible at the base rate (12 Hz) for all conditions,
 344 reflecting the general sensitivity to all visual cues rapidly changing at this frequency.

345

346 A larger identity-change response to upright human faces

347 Visual inspection of the topographical head maps of summed BCA suggests that the
 348 identity-change response appeared mainly over occipito-temporal regions with a right-
 349 hemispheric dominance (Figure 3). This was confirmed by a significant effect of ROI $F(1, 27)$
 350 $= 4.77, p = .038$, partial $\eta^2 = .15$, indicating larger activity over the RH ($M = 0.25, SD = 0.14$,
 351 $95\% CI = [0.19, 0.30]$) than LH ($M = 0.20, SD = 0.13, 95\% CI = [0.14, 0.25]$), replicating
 352 previous findings with a similar FPVS-EEG approach (Dzhelyova & Rossion, 2014b; Liu-
 353 Shuang et al., 2014; Rossion & Boremanse, 2011).

354



355
 356 Figure 3. 3D-topographical maps (posterior view) of summed baseline-corrected amplitudes
 357 and corresponding boxplots of the identity-change response for species and orientation. Black
 358 dots depict individual observations.

359 Discrimination of upright human faces elicited a strong significant response over the
 360 occipito-temporal cortex: the response peaked at the right occipito-temporal channel P10,
 361 followed by the adjacent channels P8 and PO8 (all $Z_s > 5.53$, $p < .001$), in line with previous
 362 observations (Dzhelyova & Rossion, 2014b; Liu-Shuang et al., 2014). The identity-change
 363 brain response for upright human faces was strongly reliable at the individual level, since 23
 364 out of 28 participants (i.e., $\approx 82\%$) presented significant Z-scores (i.e., $Z > 1.64$, $p < .05$) over
 365 P10. For the five remaining participants, four of them showed a significant response over at
 366 least one channel within the ROIs, and the last one over at least one posterior channel. By
 367 contrast, only 12 participants (i.e., $\approx 43\%$) presented a significant Z-score over P10 for upright
 368 monkey faces, 11 participants (i.e., $\approx 40\%$) for inverted human faces, and only 8 participants
 369 (i.e., $\approx 29\%$) for inverted monkey faces. More generally, when considering the mean response
 370 of channels included in the ROIs, 23 out of 28 participants showed a significant Z-score for
 371 upright human faces, 15 participants for upright monkey faces, 16 for inverted human faces
 372 and 8 for inverted monkey faces.

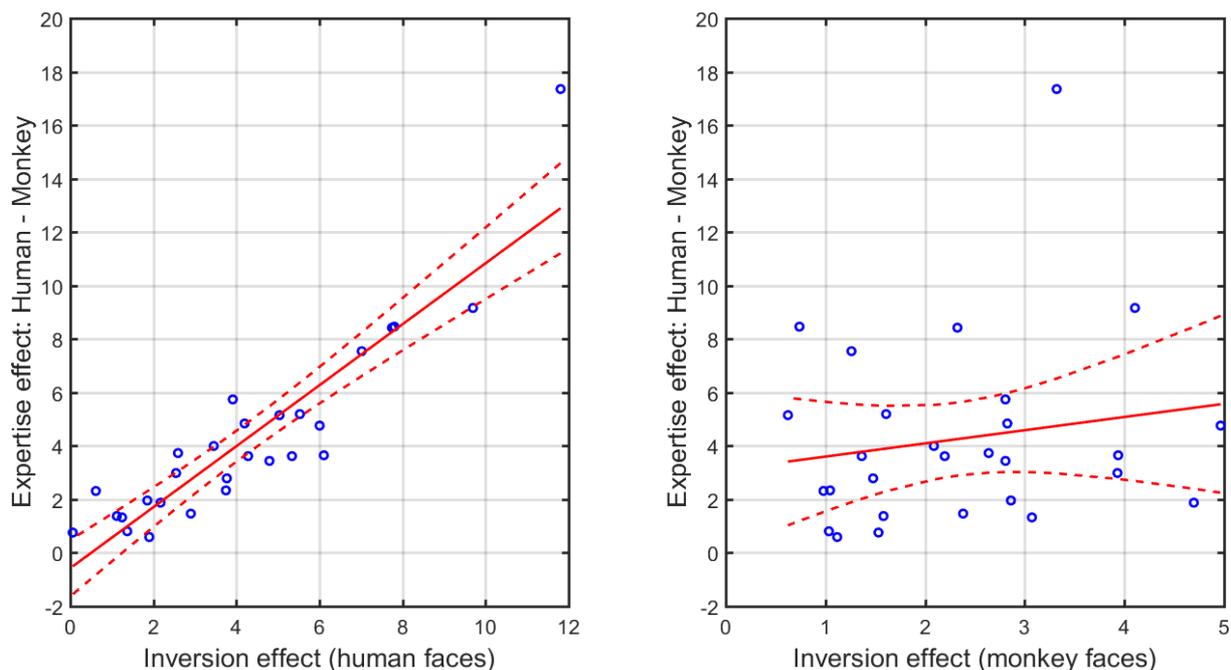
373 A significant main effect of Species ($F[1, 27] = 21.86$, $p < .001$, partial $\eta^2 = .45$)
 374 indicated that the identity-change response was stronger for human ($M = 0.29 \mu\text{V}$, $SD = 0.19$,
 375 $95\% CI = [0.22, 0.37]$) compared to monkey faces ($M = 0.15 \mu\text{V}$, $SD = 0.10$, $95\% CI = [0.11,$
 376 $0.19]$). We also found a significant effect of Orientation ($F[1, 27] = 17.04$, $p < .001$, partial η^2
 377 $= .39$) with larger amplitudes for upright ($M = 0.31 \mu\text{V}$, $SD = 0.21$, $95\% CI = [0.23, 0.39]$)
 378 compared to inverted faces ($M = 0.13 \mu\text{V}$, $SD = 0.10$, $95\% CI = [0.09, 0.17]$). These two main
 379 effects were further qualified by a significant interaction between Species and Orientation
 380 ($F[1, 27] = 5.18$, $p = .031$, partial $\eta^2 = .16$). Post hoc comparisons revealed that the response to
 381 upright human faces ($M = 0.42 \mu\text{V}$, $SD = 0.33$, $95\% CI = [0.29, 0.55]$) was significantly larger
 382 than to all other conditions (Figure 3), i.e., inverted human faces ($M = 0.17 \mu\text{V}$, $SD = 0.17$,
 383 $95\% CI = [0.11, 0.24]$, $p < .001$), upright monkey faces ($M = 0.20 \mu\text{V}$, $SD = 0.15$, $95\% CI =$
 384 $[0.14, 0.25]$, $p < .001$) and inverted monkey faces ($M = 0.10 \mu\text{V}$, $SD = 0.10$, $95\% CI = [0.06,$
 385 $0.13]$, $p < .001$). In contrast, the difference in amplitude between upright and inverted monkey
 386 faces was not significant ($p = .16$), indicating that the inversion effect was strongly reduced
 387 for monkey faces compared to human faces. There was no difference between inverted human
 388 faces and both upright and inverted monkey faces (all $ps > .38$). Note however that all
 389 conditions presented significant identity-change responses (all $ps < .006$), indicating that even
 390 inverted monkey faces elicited a discrimination response.

391 To further investigate the reliability of the “expertise effect” across participants, we
 392 examined the strength of individual differences between upright human and monkey faces.

393 For each participant, we subtracted the summed amplitude (uncorrected) obtained for upright
394 monkey faces from those obtained for upright human faces and computed Z -scores, thus
395 providing a statistical index of the expertise for human over monkey faces. This analysis
396 revealed that 22 out of 28 participants presented at least one significant channel within the
397 ROIs, that is, $\approx 79\%$ of the participants showed a significantly larger identity-change response
398 for human over monkey upright faces. Moreover, 50% of the participants showed a significant
399 Z -score on the sole electrode P10.

400 To examine the strength of the inversion effect at the individual level, a similar
401 analysis was conducted by subtracting the inverted human face condition from the upright
402 human face condition and computing Z -scores. We found that 23 out of 28 participants (i.e., \approx
403 82%) showed a reliable inversion effect for human faces over at least one electrode within the
404 ROIs. Strikingly, five of the six participants that did not show an expertise effect (i.e.,
405 significantly stronger response for human over monkey upright faces) also failed to present a
406 significant inversion effect with human faces. Besides, the size of the inversion effect for
407 human faces was related to the size of the expertise effect, explaining 81% of the variance of
408 the expertise effect (Adjusted R -squared = 0.814) as reflected by the strong correlation
409 between the two indexes ($r[26] = 0.91$, 95% $CI = [0.81, 0.96]$, $p < .001$, Figure 4). In contrast,
410 16 out of 28 participants (i.e., $\approx 57\%$) showed a reliable inversion effect with monkey faces,
411 and the size of the inversion effect for monkey faces was not correlated with the expertise
412 effect ($r[26] = 0.17$, 95% $CI = [-0.21, 0.51]$, $p = .38$), nor with the inversion effect for human
413 faces ($r[26] = 0.22$, 95% $CI = [-0.16, 0.55]$, $p = .26$). In sum, the expertise effect was larger
414 in individuals showing the stronger inversion effect with human faces, but it was dissociated
415 from the inversion effect for monkey faces. This indicates that the human expertise for face
416 individuation is highly selective to human faces (i.e., high expertise for human faces does not
417 translate into a stronger discrimination of monkey faces).

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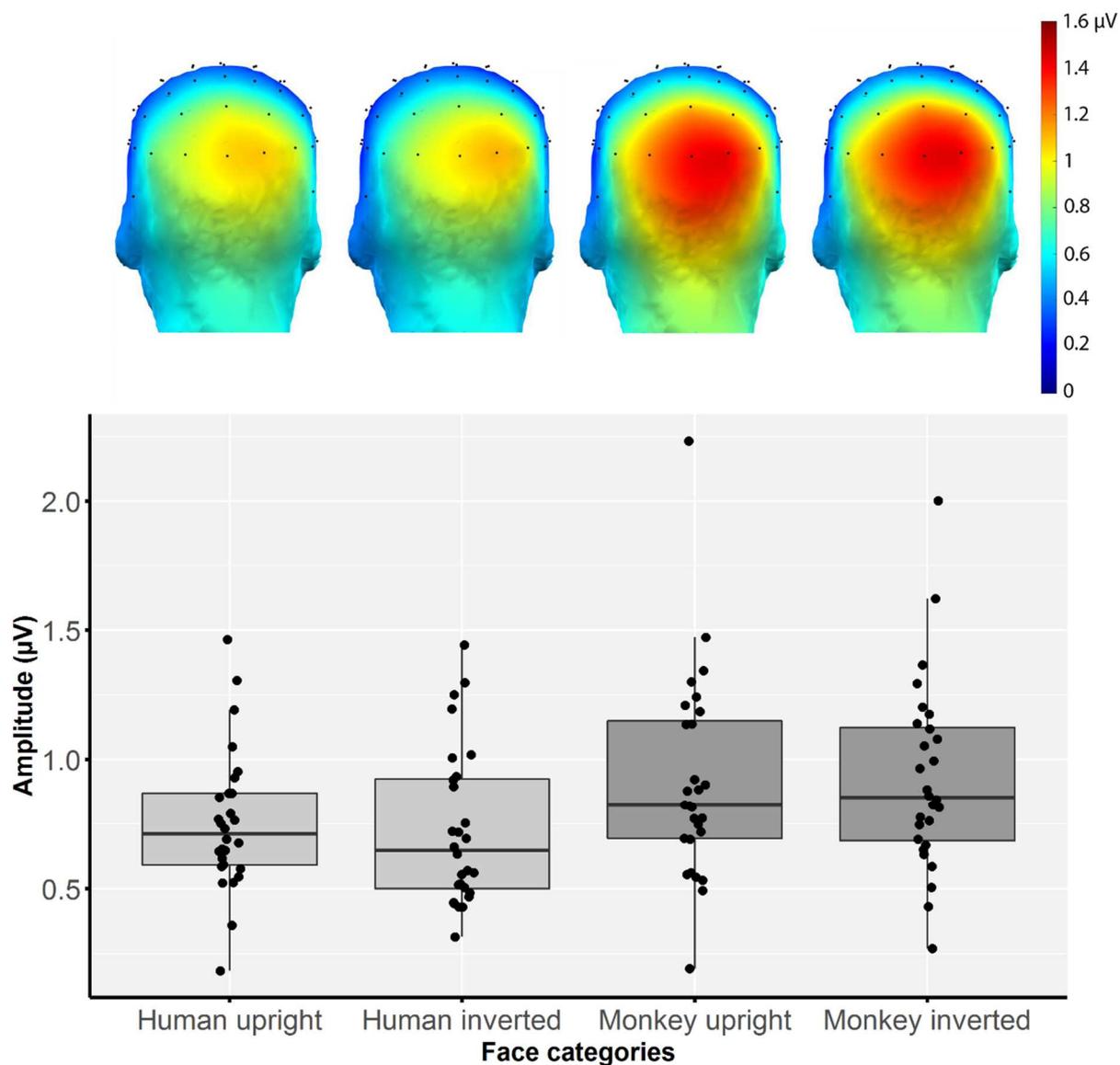
425 Figure 4. Scatter plots, regression lines (straight line), and confidence intervals (dashed line)
 426 between Z-scores for the expertise effect (i.e., upright human minus upright monkey) and the
 427 inversion effect with human faces (left), and between Z-scores of the expertise effect and the
 428 inversion effect with monkey faces (right).

429

430 The base response to the rapid stream of stimulation

431 Topographical maps of summed BCA for the base response (see Figure 5, up) revealed
 432 a larger response for monkey than human faces ($M = 0.74 \mu\text{V}$, $SD = 0.27$, $95\% CI = [0.64,$
 433 $0.84]$, $M = 0.92$, $SD = 0.37 \mu\text{V}$, $95\% CI = [0.72, 1.06]$) supported by a main effect of Species,
 434 $F(1, 27) = 30.90$, $p < .001$, partial $\eta^2 = .53$. Moreover, results also showed larger summed
 435 BCA at medial occipital sites, with a main effect of ROI ($F[1.94, 52.29] = 22.13$, $p < .001$,
 436 partial $\eta^2 = .45$), indicating a larger response over the medial occipital region ($M = 1.06$, $SD =$
 437 0.08 , $95\% CI = [0.89, 1.23]$) compared to left ($M = 0.64$, $SD = 0.05$, $95\% CI = [0.54, 0.75]$)
 438 and right ($M = 0.79$, $SD = 0.07$, $95\% CI = [0.64, 0.94]$) ROIs (both $ps < .001$). There was also
 439 a significant interaction between Species and ROI ($F[1.63, 43.94] = 9.83$, $p < .001$, partial η^2
 440 $= .27$) indicating that the advantage for monkey over human faces is larger over the medial

441 than the left and right ROIs (see Figure 5). No other effects were significant for the base
 442 response.
 443



444
 445 Figure 5. 3D-topographical maps (posterior view) of summed baseline-corrected amplitudes
 446 and corresponding boxplots of the base responses for species and orientation. Black dots
 447 depict individual observations.

448 Discussion

449 Using FPVS-EEG, we objectively (i.e., at predefined frequencies) quantified the
 450 ability of the human brain to discriminate very brief (i.e., 83 ms) changes of identity for
 451 human and monkey faces displayed in both upright and inverted orientations. In line with
 452 previous studies (Dzhelyova & Rossion, 2014a, 2014b; Liu-Shuang et al., 2014), we observed
 453 a high SNR brain response reflecting human face individuation over the occipito-temporal

454 cortex of most participants, with a right-hemispheric dominance and a strong reduction
455 following picture-plane inversion (Liu-Shuang et al., 2014). Importantly for our purpose, the
456 identity-change response was also larger for the discrimination of upright human faces
457 compared to both upright and inverted monkey faces. The mean discrimination response to
458 upright human faces was twice as large as to monkey faces, a difference that likely reflects the
459 limited environmental contact – and individuation experience – human participants had with
460 monkey faces in comparison to their extensive exposure to human faces. In addition, the
461 identity-change response was not significantly different between upright and inverted monkey
462 faces. These observations expand earlier reports of a behavioral advantage for discriminating
463 upright human faces over upright monkey faces (Dufour et al., 2006; Dufour & Petit, 2010;
464 Pascalis & Bachevalier, 1998; Pascalis et al., 2002; Scott et al., 2005; Wu et al., 2015), and of
465 a stronger impairment for human than monkey face individuation following picture-plane
466 inversion (Dufour et al., 2004; Taubert, 2009).

467 The similar identity-change response to upright monkey faces and inverted human
468 faces, both being lower than the response to upright human faces, points toward non-expert
469 visual processes for those two face formats associated with little experience. The effect of
470 picture-plane inversion reflects the disruption of high-level face identity discrimination (Liu-
471 Shuang et al., 2014), consistent with the behavioral face inversion effect (Yin, 1969, for
472 reviews see Rakover, 2013; Rossion, 2008; Valentine, 1988). It has been reported that
473 inversion induces qualitative changes in face perception hindering the processing of the global
474 face shape and relative distance between features (e.g., McKone & Yovel, 2009; Rossion,
475 2008, 2009; Yovel, 2009). Although speculative, one interpretation of the current observation
476 could be that monkey faces induce similar discrimination processes than inverted human
477 faces. Previous ERP studies consistently reported a delayed and sometimes enhanced N170
478 component in response to both inverted human faces (e.g., Caharel et al., 2006; de Haan et al.,
479 2002; Eimer, 2002; Marzi & Viggiano, 2007; Rossion et al., 1999, 2000b; Rossion &
480 Gauthier, 2002; Sadeh & Yovel, 2010) and upright monkey faces (Balas & Stevenson, 2013;
481 Carmel & Bentin, 2002; de Haan et al., 2002; Halit et al., 2003; Itier et al., 2011; Rousselet et
482 al., 2004; Wiese et al., 2009). It has been suggested that the N170 face inversion effect is
483 accounted for by the recruitment of additional neural sources involved in non-face object
484 processing (Rosburg et al., 2010; Rossion & Gauthier, 2002; for an additional eye processing
485 mechanism see also Itier, Latinus, & Taylor, 2006; Itier et al., 2011). Hence, low experience
486 with both inverted human faces and nonhuman primate faces may recruit generic object
487 recognition mechanisms that are not involved for upright human faces. In this context, it is

488 interesting to note that the base response elicited by the rapid 12-Hz stimulation sequence was
489 larger for monkey faces than human faces, as for the N170 ERP component. Like transient
490 ERPs, the base response reflects the global response of the visual system to the sudden onset
491 of face stimuli. This may be a signature that the monkey face category recruits additional
492 visual processes overall. However, it is noteworthy that a N170-like component cannot be
493 elicited with such a fast base rate since each stimulus is displayed for only ≈ 83 ms and is
494 forward- and backward-masked by other stimuli. An alternative interpretation would be that
495 the increased base response to monkey compared to human faces is driven by the lower
496 individuation abilities for monkey faces. Accordingly, identity invariance would be more
497 readily extracted across the rapid 12-Hz changes of head pose for human than monkey faces,
498 leading to a reduced brain response following adaptation to face identity for human faces only
499 (e.g., Retter & Rossion, 2016b). Although both possibilities (i.e., lack of individuation and
500 recruitment of non-face object processing mechanisms) are not mutually exclusive, they are
501 also inconsistent with the fact that we did not find an increase of the base response to
502 inverted human faces – which would have been expected in both cases. Another interpretation
503 would be that a fast train of monkey faces recruits more attentional resources than human
504 faces, in line with the typical enhancement of periodic brain activities with greater attention
505 (Morgan, Hansen, & Hillyard, 1996; Muller et al., 2006). However, note that the orthogonal
506 task was equally performed during visual streams of human and monkey faces (Table S1),
507 suggesting that participants paid similar attention to both stimulation sequences. For all these
508 reasons, further investigations are needed to determine which processes drive the increased
509 base response to monkey faces.

510 We also found that the size of individual inversion effects for human but not monkey
511 faces was predictive of individual expertise effects (i.e., amplitude difference between upright
512 human and monkey faces). These findings show that discrimination abilities as indexed by the
513 identity-change response are selective to human faces and do not contribute to higher abilities
514 for individuating other face morphologies such as monkey faces. Together with the large
515 amplitude of the response observed only for upright human faces, these results further suggest
516 qualitative differences in the processing of human faces compared to monkey faces, with
517 upright human faces recruiting dedicated processes specifically developed for this canonical
518 face format. In addition, the large variations between participants for the identity-change
519 responses to upright human faces (i.e., five participants even showed no inversion effect for
520 human faces) illustrate how the present approach is ideally suited to investigate individual

521 differences in face identity processing. Such a conclusion seems tentative since participants
522 were not behaviorally assessed. However, individual identity-change responses obtained with
523 the FPVS-EEG approach are related to behavioral performance for explicit face
524 discrimination (Xu et al., 2017), and are strongly reliable across recording sessions within a 6-
525 month interval (Stacchi, Liu-Shuang, Ramon, & Caldara, 2019). More generally, this is
526 consistent with the observation that within-subject face processing performance is highly
527 stable, and that some individual are consistently better (or worse) at discriminating faces than
528 others (Young & Burton, 2018a). Accordingly, FPVS-EEG could be used to assess individual
529 abilities for face individuation implicitly in the normal population or even in a clinical context
530 without confounding perception with decisional or motor processes.

531 Real life face individuation implies that individual faces are discriminated from other
532 faces and generalized across variable exposure conditions. Generalization refers to identity-
533 preserving image transformations, or invariance, which is a challenging computational issue
534 that primate visual systems have to deal with (DiCarlo, Zoccolan, & Rust, 2012; Thorpe, Fize,
535 & Marlot, 1996). A major strength of the current approach was thus to constrain the visual
536 system to necessarily rely on both mechanisms to individuate faces. At each stimulus onset,
537 we used a different image of the same individual with a different head pose. Therefore, the
538 identity-change response is determined by how repeated images of the same individual are
539 perceived as depicting a unique person, and how the 1.33-Hz stimuli are perceived as
540 depicting another person. Contrary to previous EEG repetition studies (Schweinberger et al.,
541 2004, 2007), the present work is thus the first to isolate a signature of high-level face
542 individuation for both human and monkey faces which cannot be accounted for by low-level
543 image-based adaptation and discrimination.

544 The current findings are theoretically sound for the recent debate on expertise in face
545 processing put forward by Young and Burton (Young & Burton, 2018c, 2018a, 2018b).
546 Young and Burton (2018a) suggest that individuating unfamiliar faces does not meet two of
547 three key criteria of expertise: high accuracy and a high degree of automaticity. They mostly
548 argue that compared to the recognition of familiar faces, the lack of knowledge about the wide
549 variability in appearance of any unfamiliar individual that arises under everyday conditions
550 leads to non-expert visual discrimination based on low-level pictorial cues (Young & Burton,
551 2018a). As a result, human participants do not reach similar accuracy levels when performing
552 face discrimination/matching tasks across variable images for unfamiliar faces (see Figure 1
553 in Young & Burton, 2018a) compared to familiar faces. However, while differences between

554 the processing of unfamiliar and familiar human faces is not questioned here, the fact that
555 humans are better at discriminating unfamiliar human compared to monkey faces suggests a
556 certain form of expertise for unfamiliar conspecific faces (Dufour et al., 2006; Dufour & Petit,
557 2010; Pascalis & Bachevalier, 1998; Pascalis et al., 2002; Scott, Shannon, & Nelson, 2005;
558 Wu et al., 2015). An important issue for such comparison of face individuation skills between
559 two stimulus sets is the use of stimuli matched for low-level visual differences. Although the
560 current findings are agnostic on accuracy for explicit judgment of face identity, they
561 nevertheless suggest that when low-level visual differences are equated (i.e., we did not
562 observe different identity-change responses between human and monkey faces in the inverted
563 orientation), humans show a clearly larger ability to individuate upright human than monkey
564 faces. In addition, our observations also qualify the view on automaticity, as the identity-
565 change response reflects automatic face discrimination during an orthogonal behavioral task.
566 The difference between human and monkey faces cannot be attributed to larger attentional
567 capture for human faces since participants performed the orthogonal task equally efficiently
568 for all experimental conditions (Table S1), and the base response, whose amplitude would be
569 enhanced by greater attentional resources (Morgan et al., 1996; Muller et al., 2006), is larger
570 for monkey faces as already mentioned. Finally, since our design measured high-level face
571 individuation processes across variable head poses presented at a very fast periodic rate, and
572 since the identity-change response to human faces was largely affected by picture-plane
573 inversion, our findings are inconsistent with the idea that unfamiliar faces are essentially
574 discriminated according to low-level pictorial cues. Altogether, the results of the present study
575 strongly suggest that human participants present a form of expertise for individuating
576 unfamiliar faces from a *familiar* face category (i.e., conspecific faces).

577 Overall, the present study provides the first EEG marker of the human selective
578 expertise to individuate upright conspecific faces, expanding previous reports on the
579 behavioral other-species effect. Moreover, this direct neural marker quantified at the
580 individual level revealed individual differences in face discrimination abilities, likely
581 reflecting idiosyncratic variations in face processing performance. While future studies should
582 further investigate the relationship between such a neural measure of rapid and automatic face
583 individuation and behavioral performance in explicit discrimination of faces as a function of
584 visual experience, the present observations yield promising tracks for delineating perceptual
585 expertise in face processing directly from brain activity.

586

587 **References**

- 588 Albonico, A., Furubacke, A., Barton, J. J. S., & Oruc, I. (2018). Perceptual efficiency and the
 589 inversion effect for faces, words and houses. *Vision Research*, *153*, 91–97.
 590 <https://doi.org/10.1016/j.visres.2018.10.008>
- 591 Alonso-Prieto, E., Belle, G. Van, Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2013). The
 592 6Hz fundamental stimulation frequency rate for individual face discrimination in the
 593 right occipito-temporal cortex. *Neuropsychologia*, *51*, 2863–2875.
 594 <https://doi.org/10.1016/j.neuropsychologia.2013.08.018>
- 595 Balas, B., & Stevenson, K. (2013). Species-specific effects of pigmentation negation on the
 596 neural response to faces. *Neuropsychologia*, *51*, 1794–1801.
 597 <https://doi.org/10.1016/j.neuropsychologia.2013.05.022>
- 598 Bell, A. J., & Sejnowski, T. I. (1995). An information-maximization approach to blind
 599 separation and blind deconvolution. *Neural Computation*, *7*, 1129–1159.
- 600 Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological
 601 studies of face perception in humans. *Journal of Cognitive Neuroscience*, *8*, 551–565.
 602 <https://doi.org/10.1162/jocn.1996.8.6.551>. Electrophysiological
- 603 Bötzel, K., Schulze, S., & Stodieck, S. R. G. (1995). Scalp topography and analysis of
 604 intracranial sources of face-evoked potentials. *Experimental Brain Research*, *104*, 135–
 605 143. <https://doi.org/10.1007/BF00229863>
- 606 Caharel, S., Fiori, N., Bernard, C., Lalonde, R., & Rebaï, M. (2006). The effects of inversion
 607 and eye displacements of familiar and unknown faces on early and late-stage ERPs.
 608 *International Journal of Psychophysiology*, *62*, 141–151.
 609 <https://doi.org/10.1016/j.ijpsycho.2006.03.002>
- 610 Carey, S. (1992). Becoming a face expert. *Philosophical Transactions of the Royal Society of*
 611 *London. B: Biological Sciences*, *335*, 95–102.
- 612 Carey, S., & Diamond, R. (1977). From piecemeal to configurational representation of faces.
 613 *Science*, *195*, 312–314. <https://doi.org/10.1126/science.831281>
- 614 Carmel, D., & Bentin, S. (2002). Domain specificity versus expertise: Factors influencing
 615 distinct processing of faces. *Cognition*, *83*, 1–29. [https://doi.org/10.1016/S0010-0277\(01\)00162-7](https://doi.org/10.1016/S0010-0277(01)00162-7)
- 617 Dahl, C. D., Logothetis, N. K., Bülthoff, H. H., & Wallraven, C. (2010). The Thatcher illusion
 618 in humans and monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *277*,
 619 2973–2981. <https://doi.org/10.1098/rspb.2010.0438>
- 620 Dahl, C. D., Logothetis, N. K., Bülthoff, H. H., & Wallraven, C. (2011). Second-order

- 621 relational manipulations affect both humans and monkeys. *PLoS ONE*, *6*, e25793.
622 <https://doi.org/10.1371/journal.pone.0025793>
- 623 Dahl, C. D., Rasch, M. J., & Chen, C. C. (2014). The other-race and other-species effects in
624 face perception - A subordinate-level analysis. *Frontiers in Psychology*, *5*, 1–9.
625 <https://doi.org/10.3389/fpsyg.2014.01068>
- 626 Dahl, C. D., Wallraven, C., Bülthoff, H. H., & Logothetis, N. K. (2009). Humans and
627 macaques employ similar face-processing strategies. *Current Biology*, *19*, 509–513.
628 <https://doi.org/10.1016/j.cub.2009.01.061>
- 629 de Haan, M., Pascalis, O., & Johnson, M. H. (2002). Specialization of neural mechanisms
630 underlying face recognition in human infants. *Journal of Cognitive Neuroscience*, *14*,
631 199–209. <https://doi.org/10.1162/089892902317236849>
- 632 Diamond, R., & Carey, S. (1986). Why faces are and are not special: an effect of expertise.
633 *Journal of Experimental Psychology: General*, *115*, 107–117.
- 634 DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How does the brain solve visual object
635 recognition? *Neuron*, *73*, 415–434. <https://doi.org/10.1016/j.neuron.2012.01.010>
- 636 Dufour, V., Coleman, M., Campbell, R., Petit, O., & Pascalis, O. (2004). On the species-
637 specificity of face recognition in human adults. *Current Psychology of Cognition*, *22*,
638 315–333.
- 639 Dufour, V., Pascalis, O., & Petit, O. (2006). Face processing limitation to own species in
640 primates: A comparative study in brown capuchins, Tonkean macaques and humans.
641 *Behavioural Processes*, *73*, 107–113. <https://doi.org/10.1016/j.beproc.2006.04.006>
- 642 Dufour, V., & Petit, O. (2010). Recognition of monkey faces by monkey experts. *Journal of*
643 *Ethology*, *28*, 231–238. <https://doi.org/10.1007/s10164-009-0174-8>
- 644 Dzhelyova, M., Jacques, C., & Rossion, B. (2017). At a single glance: Fast periodic visual
645 stimulation uncovers the spatio-temporal dynamics of brief facial expression changes in
646 the human brain. *Cerebral Cortex*, *27*, 4106–4123.
647 <https://doi.org/10.1093/cercor/bhw223>
- 648 Dzhelyova, M., & Rossion, B. (2014a). Supra-additive contribution of shape and surface
649 information to individual face discrimination as revealed by fast periodic visual
650 stimulation. *Journal of Vision*, *14*, 15–15. <https://doi.org/10.1167/14.14.15>
- 651 Dzhelyova, M., & Rossion, B. (2014b). The effect of parametric stimulus size variation on
652 individual face discrimination indexed by fast periodic visual stimulation. *BMC*
653 *Neuroscience*, *15*, 87. <https://doi.org/10.1186/1471-2202-15-87>
- 654 Eimer, M. (2002). Effects of face inversion on the structural encoding and recognition of

- 655 faces. *Cognitive Brain Research*, *10*, 145–158. <https://doi.org/10.1016/s0926->
656 6410(00)00038-0
- 657 Eimer, M. (2011). The face-sensitivity of the N170 component. *Frontiers in Human*
658 *Neuroscience*, *5*, 1–2. <https://doi.org/10.3389/fnhum.2011.00119>
- 659 Gajewski, P. D., & Stoerig, P. (2011). N170 - an index of categorical face perception?: An
660 ERP study of human, nonhuman primate, and dog faces. *Journal of Psychophysiology*,
661 *25*, 174–179. <https://doi.org/10.1027/0269-8803/a000057>
- 662 Gao, X., Vuong, Q. C., & Rossion, B. (2018). The cortical face network of the prosopagnosic
663 patient PS with fast periodic stimulation in fMRI. *Cortex*.
664 <https://doi.org/10.1016/j.cortex.2018.11.008>
- 665 Hagen, S., & Tanaka, J. W. (2019). Examining the neural correlates of within-category
666 discrimination in face and non-face expert recognition. *Neuropsychologia*, *124*, 44–54.
667 <https://doi.org/10.1016/j.neuropsychologia.2019.01.005>
- 668 Halit, H., de Haan, M., & Johnson, M. H. (2003). Cortical specialisation for face processing:
669 Face-sensitive event-related potential components in 3- and 12-month-old infants.
670 *NeuroImage*, *19*, 1180–1193. [https://doi.org/10.1016/S1053-8119\(03\)00076-4](https://doi.org/10.1016/S1053-8119(03)00076-4)
- 671 Itier, R. J., Alain, C., Sedore, K., & McIntosh, A. R. (2007). Early face processing specificity:
672 It's in the eyes! *Journal of Cognitive Neuroscience*, *19*, 1815–1826.
673 <https://doi.org/10.1162/jocn.2007.19.11.1815>
- 674 Itier, R. J., Latinus, M., & Taylor, M. J. (2006). Face, eye and object early processing: What is
675 the face specificity? *NeuroImage*, *29*, 667–676.
676 <https://doi.org/10.1016/j.neuroimage.2005.07.041>
- 677 Itier, R. J., Van Roon, P., & Alain, C. (2011). Species sensitivity of early face and eye
678 processing. *NeuroImage*, *54*, 705–713. <https://doi.org/10.1016/j.neuroimage.2010.07.031>
- 679 Jacques, C., Retter, T. L., & Rossion, B. (2016). A single glance at natural face images
680 generate larger and qualitatively different category-selective spatio-temporal signatures
681 than other ecologically-relevant categories in the human brain. *NeuroImage*, *137*, 21–33.
682 <https://doi.org/10.1016/j.neuroimage.2016.04.045>
- 683 Kasinski, A., Florek, A., & Schmidt, A. (2008). The PUT face database. *Image Processing*
684 *and Communications*, *13*, 59–64.
- 685 Kuefner, D., Macchi Cassia, V., Picozzi, M., & Bricolo, E. (2008). Do all kids look alike?
686 Evidence for an other-age effect in adults. *Journal of Experimental Psychology. Human*
687 *Perception and Performance*, *34*, 811–817. <https://doi.org/10.1037/0096-1523.34.4.811>
- 688 Leleu, A., Dzhelyova, M., Rossion, B., Brochard, R., Durand, K., Schaal, B., & Baudouin, J.-

- 689 Y. (2018). Tuning functions for automatic detection of brief changes of facial expression
690 in the human brain. *NeuroImage*, *179*, 235–251.
691 <https://doi.org/10.1016/j.neuroimage.2018.06.048>
- 692 Leleu, A., Favre, E., Yailian, A., Fumat, H., Klamm, J., Amado, I., ... Demily, C. (2019). An
693 implicit and reliable neural measure quantifying impaired visual coding of facial
694 expression: evidence from the 22q11.2 deletion syndrome. *Translational Psychiatry*,
695 *9*(1). <https://doi.org/10.1038/s41398-019-0411-z>
- 696 Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2014). An objective index of individual face
697 discrimination in the right occipito-temporal cortex by means of fast periodic oddball
698 stimulation. *Neuropsychologia*, *52*, 57–72.
699 <https://doi.org/10.1016/j.neuropsychologia.2013.10.022>
- 700 Liu-Shuang, J., Torfs, K., & Rossion, B. (2016). An objective electrophysiological marker of
701 face individualisation impairment in acquired prosopagnosia with fast periodic visual
702 stimulation. *Neuropsychologia*, *83*, 100–113.
703 <https://doi.org/10.1016/j.neuropsychologia.2015.08.023>
- 704 Marzi, T., & Viggiano, M. P. (2007). Interplay between familiarity and orientation in face
705 processing: An ERP study. *International Journal of Psychophysiology*, *65*, 182–192.
706 <https://doi.org/10.1016/j.ijpsycho.2007.04.003>
- 707 Maurer, D., & Werker, J. F. (2014). Perceptual narrowing during infancy: A comparison of
708 language and faces. *Developmental Psychobiology*, *56*, 154–178.
709 <https://doi.org/10.1002/dev.21177>
- 710 McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: An
711 ambiguity associated with analysis of variance models. *Electroencephalography and*
712 *Clinical Neurophysiology*, *62*, 203–208.
- 713 McGugin, R. W., Newton, A. T., Gore, J. C., & Gauthier, I. (2014). Robust expertise effects
714 in right FFA. *Neuropsychologia*, *63*, 135–144.
715 <https://doi.org/10.1016/j.neuropsychologia.2014.08.029>
- 716 McKone, E., & Yovel, G. (2009). Why does picture-plane inversion sometimes dissociate
717 perception of features and spacing in faces, and sometimes not? Toward a new theory of
718 holistic processing. *Psychonomic Bulletin & Review*, *16*, 778–797.
719 <https://doi.org/10.3758/PBR.16.5.778>
- 720 Meissner, C. a., & Brigham, J. C. (2001). Thirty years of investigating the own-race bias in
721 memory for faces: A meta-analytic review. *Psychology, Public Policy, and Law*, *7*, 3–35.
722 <https://doi.org/10.1037/1076-8971.7.1.3>

- 723 Mondloch, C. J., Maurer, D., & Ahola, S. (2006). Becoming a face expert. *Psychological*
724 *Science*, *17*, 930–934. <https://doi.org/10.1111/j.1467-9280.2006.01806.x>
- 725 Morgan, S. T., Hansen, J. C., & Hillyard, S. A. (1996). Selective attention to stimulus location
726 modulates the steady-state visual evoked potential. *Proceedings of the National Academy*
727 *of Sciences*, *93*, 4770–4774. <https://doi.org/10.1073/pnas.93.10.4770>
- 728 Muller, M. M., Andersen, S., Trujillo, N. J., Valdes-Sosa, P., Malinowski, P., & Hillyard, S.
729 A. (2006). Feature-selective attention enhances color signals in early visual areas of the
730 human brain. *Proceedings of the National Academy of Sciences*, *103*, 14250–14254.
731 <https://doi.org/10.1073/pnas.0606668103>
- 732 Or, C. C. F., Retter, T. L., & Rossion, B. (2019). The contribution of color information to
733 rapid face categorization in natural scenes. *Journal of Vision*, *19*, 1–20.
734 <https://doi.org/10.1167/19.5.20>
- 735 Pascalis, O., & Bachevalier, J. (1998). Face recognition in primates: A cross-species study.
736 *Behavioural Processes*, *43*, 87–96. [https://doi.org/10.1016/S0376-6357\(97\)00090-9](https://doi.org/10.1016/S0376-6357(97)00090-9)
- 737 Pascalis, O., de Haan, M., & Nelson, C. A. (2002). Is face processing species-specific during
738 the first year of life? *Science*, *296*, 1321–1323. <https://doi.org/10.1126/science.1070223>
- 739 Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson JR., R., ... Taylor,
740 M. J. (2000). Guidelines for using human event-related potentials to study cognition:
741 Recording standards and publication criteria. *Psychophysiology*, *37*, 127–152.
742 <https://doi.org/10.1111/1469-8986.3720127>
- 743 Poncet, F., Baudouin, J. Y., Dzhelyova, M. P., Rossion, B., & Leleu, A. (2019). Rapid and
744 automatic discrimination between facial expressions in the human brain.
745 *Neuropsychologia*, *129*(March), 47–55.
746 <https://doi.org/10.1016/j.neuropsychologia.2019.03.006>
- 747 Rakover, S. S. (2013). Explaining the face-inversion effect: The face-scheme incompatibility
748 (FSI) model. *Psychonomic Bulletin and Review*, *20*, 665–692.
749 <https://doi.org/10.3758/s13423-013-0388-1>
- 750 Retter, T. L., Jiang, F., Webster, M. A., & Rossion, B. (2018). Dissociable effects of inter-
751 stimulus interval and presentation duration on rapid face categorization. *Vision Research*,
752 *145*(February), 11–20. <https://doi.org/10.1016/j.visres.2018.02.009>
- 753 Retter, T. L., & Rossion, B. (2016a). Uncovering the neural magnitude and spatio-temporal
754 dynamics of natural image categorization in a fast visual stream. *Neuropsychologia*, *91*,
755 9–28. <https://doi.org/10.1016/j.neuropsychologia.2016.07.028>
- 756 Retter, T. L., & Rossion, B. (2016b). Visual adaptation provides objective

- 757 electrophysiological evidence of facial identity discrimination. *Cortex*, *80*, 35–50.
758 <https://doi.org/10.1016/j.cortex.2015.11.025>
- 759 Rhodes, M. G., & Anastasi, J. S. (2012). The own-age bias in face recognition: A meta-
760 analytic and theoretical review. *Psychological Bulletin*, *138*, 146–174.
761 <https://doi.org/10.1037/a0025750>
- 762 Rosburg, T., Ludwig, E., Dümpelmann, M., Alba-Ferrara, L., Urbach, H., & Elger, C. E.
763 (2010). The effect of face inversion on intracranial and scalp recordings of event-related
764 potentials. *Psychophysiology*, *47*, 147–157. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-8986.2009.00881.x)
765 [8986.2009.00881.x](https://doi.org/10.1111/j.1469-8986.2009.00881.x)
- 766 Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception.
767 *Acta Psychologica*, *128*, 274–289. <https://doi.org/10.1016/j.actpsy.2008.02.003>
- 768 Rossion, B. (2009). Distinguishing the cause and consequence of face inversion: the
769 perceptual field hypothesis. *Acta Psychologica*, *132*, 300–312.
770 <https://doi.org/10.1016/j.actpsy.2009.08.002>
- 771 Rossion, B. (2014). Understanding face perception by means of human electrophysiology.
772 *Trends in Cognitive Sciences*, *18*, 310–318. <https://doi.org/10.1016/j.tics.2014.02.013>
- 773 Rossion, B. (2018). Humans are visual experts at unfamiliar face recognition. *Trends in*
774 *Cognitive Sciences*, *22*, 471–472. <https://doi.org/10.1016/j.tics.2018.03.002>
- 775 Rossion, B., & Boremanse, A. (2011). Robust sensitivity to facial identity in the right human
776 occipito-temporal cortex as revealed by steady-state visual-evoked potentials. *Journal of*
777 *Vision*, *11*, 16–16. <https://doi.org/10.1167/11.2.16>
- 778 Rossion, B., Curran, T., & Gauthier, I. (2002). A defense of the subordinate-level expertise
779 account for the N170 component. *Cognition*, *85*, 189–196.
780 [https://doi.org/10.1016/S0010-0277\(02\)00101-4](https://doi.org/10.1016/S0010-0277(02)00101-4)
- 781 Rossion, B., Delvenne, J. F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., &
782 Guérit, J. M. (1999). Spatio-temporal localization of the face inversion effect: an event-
783 related potentials study. *Biological Psychology*, *50*, 173–189.
784 [https://doi.org/10.1016/S0301-0511\(99\)00013-7](https://doi.org/10.1016/S0301-0511(99)00013-7)
- 785 Rossion, B., & Gauthier, I. (2002). How does the brain process upright and inverted faces?
786 *Behavioral and Cognitive Neuroscience Reviews*, *1*, 63–75.
787 <https://doi.org/10.1177/1534582302001001004>
- 788 Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck,
789 M. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted
790 faces but not to inverted objects: an electrophysiological account of face-specific

- 791 processes in the human brain. *NeuroReport*, *11*, 69–72.
792 <https://doi.org/10.1097/00001756-200001170-00014>
- 793 Rossion, B., & Jacques, C. (2011). The N170: understanding the time-course of face
794 perception in the human brain. In *The Oxford Handbook of ERP Components* (pp. 115–
795 142). Oxford, UK, UK: Oxford University Press.
796 <https://doi.org/10.1093/oxfordhb/9780195374148.013.0064>
- 797 Rossion, B., & Michel, C. (2011). An experience-based holistic account of the other-race face
798 effect. In G. Rhodes, A. Calder, M. H. Johnson, & J. V Haxby (Eds.), *Oxford Handbook*
799 *of Face Perception* (pp. 1–40). Oxford, UK: Oxford University Press.
800 <https://doi.org/10.1093/oxfordhb/9780199559053.013.0012>
- 801 Rossion, B., Torfs, K., Jacques, C., & Liu-Shuang, J. (2015). Fast periodic presentation of
802 natural images reveals a robust face-selective electrophysiological response in the human
803 brain. *Journal of Vision*, *15*, 1–18. <https://doi.org/10.1167/15.1.18>
- 804 Rousselet, G. A., Mace, M. J.-M., & Fabre-Thorpe, M. (2004). Animal and human faces in
805 natural scenes: How specific to human faces is the N170 ERP component? *Journal of*
806 *Vision*, *4*, 2–2. <https://doi.org/10.1167/4.1.2>
- 807 Sadeh, B., & Yovel, G. (2010). Why is the N170 enhanced for inverted faces? An ERP
808 competition experiment. *NeuroImage*, *53*, 782–789.
809 <https://doi.org/10.1016/j.neuroimage.2010.06.029>
- 810 Sampat, M. P., Wang, Z., Gupta, S., Bovik, A. C., & Markey, M. K. (2009). Complex wavelet
811 structural similarity: A new image similarity index. *IEEE Transactions on Image*
812 *Processing*, *18*, 2385–2401.
- 813 Schweinberger, S. R., Huddy, V., & Burton, A. M. (2004). N250r: A face-selective brain
814 response to stimulus repetitions. *NeuroReport*, *15*, 1501–1505.
815 <https://doi.org/10.1097/01.wnr.0000131675.00319.42>
- 816 Schweinberger, S. R., Kaufmann, J. M., Moratti, S., Keil, A., & Burton, A. M. (2007). Brain
817 responses to repetitions of human and animal faces, inverted faces, and objects - An
818 MEG study. *Brain Research*, *1184*, 226–233.
819 <https://doi.org/10.1016/j.brainres.2007.09.079>
- 820 Scott, L. S., & Fava, E. (2013). The own-species face bias: A review of developmental and
821 comparative data. *Visual Cognition*, *21*, 1364–1391.
822 <https://doi.org/10.1080/13506285.2013.821431>
- 823 Scott, L. S., Shannon, R. W., & Nelson, C. A. (2005). Behavioral and electrophysiological
824 evidence of species-specific face processing. *Cognitive, Affective & Behavioral*

- 825 *Neuroscience*, 5, 405–416. <https://doi.org/https://doi.org/10.3758/CABN.5.4.405>
- 826 Simpson, E. A., Jakobsen, K. V., Damon, F., Suomi, S. J., & Ferrari, P. F. (2017). Face
827 detection and the development of own-species bias in infant macaques. *Child*
828 *Development*, 88, 103–113. <https://doi.org/10.1111/cdev.12565>
- 829 Stacchi, L., Liu-Shuang, J., Ramon, M., & Caldara, R. (2019). Reliability of individual
830 differences in neural face identity discrimination. *NeuroImage*, 189, 468–475.
831 <https://doi.org/10.1016/J.NEUROIMAGE.2019.01.023>
- 832 Stacchi, L., Ramon, M., Lao, J., & Caldara, R. (2019). Neural representations of faces are
833 tuned to eye movements. *Journal of Neuroscience*, 39, 4113–4123.
834 <https://doi.org/10.1523/jneurosci.2968-18.2019>
- 835 Sugita, Y. (2008). Face perception in monkeys reared with no exposure to faces. *Proceedings*
836 *of the National Academy of Sciences*, 105, 394–398.
837 <https://doi.org/10.1073/pnas.0706079105>
- 838 Sunday, M. A., & Gauthier, I. (2018). Face expertise for unfamiliar faces: A commentary on
839 Young and Burton’s “are we face experts?” *Journal of Expertise*, 1, 130–135.
- 840 Taubert, J. (2009). Chimpanzee faces are “special” to humans. *Perception*, 38, 343–356.
841 <https://doi.org/10.1068/p6254>
- 842 Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system.
843 *Nature*, 381, 520–522. <https://doi.org/10.1038/381520a0>
- 844 Valentine, T. (1988). Upside-down faces: a review of the effect of inversion upon face
845 recognition. *British Journal of Psychology*, 79, 471–491. [https://doi.org/10.1111/j.2044-](https://doi.org/10.1111/j.2044-8295.1988.tb02747.x)
846 [8295.1988.tb02747.x](https://doi.org/10.1111/j.2044-8295.1988.tb02747.x)
- 847 White, D., Phillips, P. J., Hahn, C. A., Hill, M., & O’Toole, A. J. (2015). Perceptual expertise
848 in forensic facial image comparison. *Proceedings of the Royal Society B: Biological*
849 *Sciences*, 282, 20151292. <https://doi.org/10.1098/rspb.2015.1292>
- 850 Wiese, H., Stahl, J., & Schweinberger, S. R. (2009). Configural processing of other-race faces
851 is delayed but not decreased. *Biological Psychology*, 81, 103–109.
852 <https://doi.org/10.1016/j.biopsycho.2009.03.002>
- 853 Wu, R., Nako, R., Band, J., Pizzuto, J., Ghoreishi, Y., Scerif, G., & Aslin, R. (2015). Rapid
854 attentional selection of non-native stimuli despite perceptual narrowing. *Journal of*
855 *Cognitive Neuroscience*, 27, 2299–2307. https://doi.org/10.1162/jocn_a_00857
- 856 Xu, B., Liu-Shuang, J., Rossion, B., & Tanaka, J. W. (2017). Individual differences in face
857 identity processing with fast periodic visual stimulation. *Journal of Cognitive*
858 *Neuroscience*, 29, 1368–1377. https://doi.org/doi:10.1162/jocn_a_01126

- 859 Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*,
860 141–145. <https://doi.org/10.1037/h0027474>
- 861 Young, A. W., & Burton, A. M. (2018a). Are we face experts? *Trends in Cognitive Sciences*,
862 *22*, 100–110. <https://doi.org/10.1016/j.tics.2017.11.007>
- 863 Young, A. W., & Burton, A. M. (2018b). The limits of expertise in face recognition:
864 Response to Sunday and Gauthier’s “face expertise for unfamiliar faces: A commentary
865 on Young and Burton’s ‘are we face experts?’” *Journal of Expertise*, *1*, 1–6.
- 866 Young, A. W., & Burton, A. M. (2018c). What we see in unfamiliar faces: A response to
867 Rossion. *Trends in Cognitive Sciences*, *22*, 472–473.
868 <https://doi.org/10.1016/j.tics.2018.03.008>
- 869 Yovel, G. (2009). The shape of facial features and the spacing among them generate similar
870 inversion effects: A reply to Rossion (2008). *Acta Psychologica*, *13*, 293–299.
871 <https://doi.org/10.1016/j.actpsy.2009.07.009>
872