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An ecological measure of rapid and automatic face-sex categorization

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Diane Rekow: Data Curation, Formal Analysis, Investigation, Visualization, Writing - Original Draft, Writing - Review & Editing. **Jean-Yves Baudouin:** Funding Acquisition, Methodology, Project Administration, Supervision, Writing - Review & Editing. **Bruno Rossion:** Methodology, Writing - Review & Editing. **Arnaud Leleu:** Funding Acquisition, Methodology, Formal Analysis, Project Administration, Supervision, Writing - Original Draft, Writing - Review & Editing.

Abstract

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2 Sex categorization is essential for mate choice and social interactions in many animal species. In
3 humans, sex categorization is readily performed from the face. However, clear neural markers of
4 face-sex categorization, i.e. common responses to widely variable individuals from one sex, have not
5 been identified so far in humans. To isolate a direct signature of rapid and automatic face-sex
6 categorization generalized across a wide range of variable exemplars, we recorded scalp
7 electroencephalogram (EEG) from 32 participants (16 females) while they were exposed to variable
8 natural face images from one sex alternating at a rapid rate of 6 Hz (i.e., 6 images per second).
9 Images from the other sex were inserted every 6th stimulus (i.e., at a 1-Hz rate). A robust
10 categorization response to both sex contrasts emerged at 1 Hz and harmonics in the EEG frequency
11 spectrum over the occipito-temporal cortex of most participants. The response was larger for female
12 faces presented among male faces than the reverse, suggesting that the two sex categories are not
13 equally homogenous. This asymmetrical response pattern disappeared for upside-down faces, ruling
14 out the contribution of low-level physical variability across images. Overall, these observations
15 demonstrate that sex categorization occurs automatically after a single glance at natural face images
16 and can be objectively isolated and quantified in the human brain within a few minutes.
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32 **Keywords:** sex categorization, natural face images, EEG, fast periodic visual stimulation, frequency-
33 tagging
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1. Introduction

In many animal species, sex recognition is essential for social interactions and mate choice. In humans, sex recognition is readily achieved from an analysis of the facial structure (Bruce and Young, 1998). Face sex is classified efficiently from pictures of faces (O’Toole et al., 1998; Wild et al., 2000) even when the images are partially degraded (Cellerino et al., 2004), occluded (Bruce et al., 1993; Dupuis-Roy et al., 2009), silhouetted (Davidenko, 2007) or when sex judgments are performed simultaneously with an attentional demanding task (Reddy et al., 2004). This apparent simplicity may result from the nature of face-sex categorization, which, unlike other face-related categorizations (e.g., age, expression, “race”), is binary (Armann and Bühlhoff, 2012; Freeman et al., 2010).

Over the last decades, a large body of research has thoroughly investigated the diagnostic cues for face-sex judgments. The first behavioral studies showed that all isolated internal facial parts carry information about the sex of a face (Chronicle et al., 1995), with each a different weight (i.e., eyes then mouth then nose; Brown and Perrett, 1993). Face outline alone is also diagnostic for face sex (Yamaguchi et al., 1995). More recent studies revealed the role of skin texture and color. They found that local contrast (Russell, 2003), overall contrast (Nestor and Tarr, 2008; Russell, 2005) and skin color variations along the red-green channel (Dupuis-Roy et al., 2009; Nestor and Tarr, 2008) contribute to face-sex classification. In addition, although face sex is well identified from isolated features, “none of these factors is sufficient on its own” (Burton et al., 1993). Indeed, when facial parts are inserted within the whole face, their order of importance changes (Brown and Perrett, 1993; Yamaguchi et al., 1995), showing that face-sex categorization also relies on interactive processing of these parts. Along this line, the relative distance between face features biases sex judgments (Burton et al., 1993; Roberts and Bruce, 1988), and picture-plane inversion disrupts sex categorization performance (Bruce et al., 1993; Bruce and Langton, 1994; Reddy et al., 2004; Zhao and Hayward, 2010). Furthermore, recognizing the sex of the top half of a face is poorer when it is aligned with the bottom half of a face from the opposite sex, the so-called composite face illusion (Young et al., 1987; for a review, see Rossion, 2013) applied to face sex (Baudouin and Humphreys, 2006; Zhao and Hayward, 2010).

Intriguingly, converging evidence indicates that the contribution of the aforementioned cues also depends on incidental exposure conditions. For instance, while it has been shown that achromatic information is four times more useful than chromatic information (Dupuis-Roy et al., 2018), face color is more decisive for full-front than three-quarter views (Hill et al., 1995). Face-sex judgment is also impacted by spatial location, with faces respectively appearing more female when displayed in the left visual field and more male when displayed in the upper visual field (Afriz et al.,

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2010). In contrast, face-sex aftereffect studies (i.e., perceiving the opposite sex in an androgynous face after being adapted to a face from one sex, Webster et al., 2004) point to high-level sex categorization mechanisms by showing aftereffects across viewpoints, contrast polarity or left-right orientation (Davidenko, 2007), and even after body – instead of face – adaptation (Ghuman et al., 2010). Altogether, these findings question whether face-sex categorization is strongly context-dependent (i.e., according to exposure conditions and available features) or whether face-sex-selective processes are rather invariant to physical changes (i.e., across exposure conditions) and physiognomic differences (i.e., across individual faces).

In principle, neural measures are well adapted to tackle this issue. However, so far, neuroimaging and electrophysiological studies have struggled to isolate clear neural markers of face-sex categorization. Functional imaging studies found sex-selective activity distributed across numerous brain regions within the core and extended (Haxby et al., 2000) face processing networks (Kaul et al., 2011; Ng et al., 2006; Podrebarac et al., 2013; Sergent et al., 1992) and other cortical areas (Ino et al., 2010; Ng et al., 2006; Podrebarac et al., 2013), but no reliable pattern emerged across studies. Similarly, no consensus arose from the investigation of face-sex processing using scalp electroencephalography (EEG) and the standard event-related potential (ERP) approach. For instance, some studies observed a modulation of the well-known N170 face-sensitive occipito-temporal ERP component (Bentin et al., 1996) by sex information (Carrito et al., 2018; Cellierino et al., 2007; Kovács et al., 2006; Sun et al., 2010), but others did not (Ito and Urland, 2005; Kloth et al., 2010, 2010; Mouchetant-Rostaing et al., 2000). More generally, the scalp topography, polarity and latency of sex-sensitive ERPs are inconsistent across studies, from effects observed as early as 140 ms after stimulus-onset over frontal and central locations (Mouchetant-Rostaing et al., 2000; 2003; Sun et al., 2010), to others around 200 ms over sparse regions (Dickter and Bartholow, 2007; Ito and Urland, 2005, 2003; Kecskes-Kovacs et al., 2013; Yokoyama et al., 2014; Zhang et al., 2016), and until 300 to 400 ms at occipito-temporal sites (Rakić et al., 2018). A major limitation of these studies is that they generally used homogenous sets of face stimuli (e.g., segmented full front faces devoid of external features). While this manipulation is applied to minimize differences between male and female faces, it also limits the measure of sex categorization from all cues available in natural circumstances. In addition, these studies used a post-hoc contrast between two responses to the sudden onset of male and female faces from a blank baseline (i.e., a uniform visual field) and thus did not directly measure a *differential* response to a change of face sex.

Here we aimed at capturing rapid and automatic human sex categorization across variable exposure conditions and individual faces. To do so, we presented widely variable natural images using fast periodic visual stimulation (FPVS) while recording scalp EEG (Rossion et al., 2015).

1 Specifically, unsegmented face images from one sex were presented at a 6-Hz base rate (i.e., 6
2 images per second, ≈ 167 ms per image, one fixation) and faces from the other sex were interspersed
3 every 6th image, introducing single-glance changes of face sex at 6 Hz/6 images = 1 Hz (Figure 1).
4 Hence, distinct brain responses were tagged at two frequencies within the same stimulation
5 sequence and quantified in the EEG frequency spectrum at the exact same frequencies and their
6 harmonics (i.e., integer multiples). On the one hand, the general visual response (i.e., 6 Hz and
7 harmonics) is elicited by all face images (i.e., from both sexes) and reflects the processing of rapid
8 changes in both low-level (e.g., contrast) and higher-level (e.g., face identity) cues. On the other
9 hand, and most interestingly, the face-sex categorization response (i.e., 1 Hz and harmonics) is
10 elicited by the periodic occurrence of faces from the other sex and captures high-level sex-selective
11 neural activity, since it only appears if face images are discriminated according to sex, and if this
12 direct differential response is generalized across the widely variable exemplars of faces (Figure 1 &
13 S1). In other words, we measured a selective response to a change of face sex uncontaminated by
14 visual processes shared by faces from both sexes (which project to the general response) or
15 transiently (i.e., non-periodically) elicited by a subset of faces. This crucial property of the approach
16 thus allows using various faces unsegmented from their natural background to measure a rich
17 categorization response unaffected by incidental exposure conditions and facial cues (i.e., every
18 diagnostic cue for face sex is available, even those generally removed in experimental settings; e.g.,
19 hairstyle, beard, make-up, jewelry; see Rossion et al., 2015 for this approach applied to generic face
20 categorization). Importantly, participants performed a non-periodic and orthogonal cross-detection
21 task to isolate automatic categorization of face sex exempt from variable response-related processes.
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38 **2. Material and methods**

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40 We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria,
41 whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all
42 measures in the study. No part of the study procedures or analyses was pre-registered in an
43 institutional registry prior to the research being conducted.
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48 **2.1. Participants**

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50 Thirty-two healthy participants (16 females, range: 18–31 years-old, mean \pm SD: 22 \pm 3.2; 22 right-
51 handed) were tested (sample size for each group was established according to previous FPVS-EEG
52 studies; e.g., Retter and Rossion, 2016; and was in fact higher than in most previous studies).
53 According to inclusion/exclusion criteria (determined prior to data analysis), all reported normal or
54 corrected-to-normal visual acuity and none reported any history of neurological or psychiatric
55 disorder. They provided written informed consent prior to beginning the experiment and were
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1 financially compensated for their participation. They were not informed of the specific aim of the
2 study (face-sex categorization) before the experiment, and a full interview was conducted at the end
3 to explain the whys and wherefores of the current study. No participant declared being aware of the
4 aim of the study prior to beginning. Testing was conducted in accordance with the Declaration of
5 Helsinki.
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8 9 **2.2. Stimuli**

10 We used 66 color natural photographs of Caucasian male (33) and female (33) faces in various
11 displays (Figure 1A, full set available in Figure S1; subset of stimuli used in e.g., Retter and Rossion,
12 2016). Faces were unsegmented from their background, i.e., embedded in their original visual scene.
13 Each image depicted one individual face, more or less off-centered, and varying in size, viewpoints,
14 lighting condition and background. Individuals were also variable in terms of age (\approx from 20 to 50
15 years old), facial expression, hairstyle, glasses apparatus, make-up or jewelry for females, and
16 shaving for males. Stimuli were cropped to a square and sized to 300×300 pixels. They were
17 presented on a grey background (i.e., 128/255 in greyscale) at the center of a 24-inch LED screen (60
18 Hz refresh rate, resolution: 1920×1080 pixels). From a distance of 57 cm, they covered roughly 8.3°
19 of visual angle.
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22 **2.3. Design and procedure**

23 Single-glance face-sex categorization was implicitly measured in the brain using fast periodic visual
24 stimulation (FPVS) with EEG (Norcia et al., 2015, for a review). The design was adapted from previous
25 studies that successfully isolated and quantified a neural generic face categorization response (i.e.,
26 vs. non-face objects; Jacques et al., 2016; Retter and Rossion, 2016; Rossion et al., 2015) or a familiar
27 face identity recognition response (Zimmermann et al., 2019). Here, face images from one sex were
28 presented without inter-stimulus interval during fast stimulation sequences at a 6-Hz base rate (i.e.,
29 6 images per second, ≈ 167 ms per image, Figure 1B). Faces from the other sex were periodically
30 inserted every 6th stimulus (i.e., at a lower frequency of $6 \text{ Hz}/6 \text{ images} = 1 \text{ Hz}$; 1 second between two
31 changes of face sex). Therefore, given that visual categorization responses can be recorded at various
32 frequencies in EEG frequency-tagging designs as soon as sufficient time is available to process the
33 information (e.g., Retter and Rossion, 2016), and since behavioral face-sex classification can be
34 achieved in less than 600 ms with our stimulus set (see Supplementary Information and Table S2),
35 this interval of 1 second between 2 changes of face sex allows ample time for the face-sex
36 categorization response to unfold. Two distinct brain responses were thus identified and quantified
37 in the EEG amplitude spectrum using frequency-domain analysis: (1) a general visual response at 6 Hz
38 and harmonics (i.e., integer multiples) elicited by all face images; (2) a face-sex categorization
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1 response at 1 Hz and harmonics elicited by the periodic occurrence of face images from the other
 2 sex. When interviewed after the experiment, all participants reported having noticed the
 3 presentation of individual faces of both sexes, but none detected the periodic contrasts of face sex
 4 during the sequences.
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7 Stimuli were presented during 35-second-long stimulation sequences starting with a variable
 8 pre-stimulation interval of 0.5 to 1.5 seconds of uniform grey screen, followed by a 2-second fade-in
 9 of increasing contrast modulation depth (0 to 100%, to reduce eye-blinks or muscular artifacts
 10 elicited by the sudden appearance of flickering images). The full-contrast sequence then lasted 30
 11 seconds and ended with an additional 1-second fade-out of decreasing contrast modulation depth
 12 (100% to 0) followed by a variable post-stimulation interval of 0.5 to 1.5 seconds. Stimulation
 13 sequences presented either upright male (M) or female (F) faces at the rapid 6-Hz base rate and the
 14 other sex appeared at the face-sex categorization rate of 1 Hz. For both frequencies, M or F faces
 15 were randomly chosen among their respective stimulus sets. For the base stimuli, the 33 exemplars
 16 were randomly picked at the beginning of each sequence and repeated after one presentation loop
 17 ended (i.e., after all 33 exemplars had been used, a new draw was made). As a control condition,
 18 stimuli were also presented upside-down (inverted condition). Four conditions corresponding to the
 19 2 sex contrasts (M vs. F, F vs. M) \times 2 orientations (upright and inverted) were repeated 4 times
 20 throughout the experiment. The 16 resulting sequences were divided into 4 blocks of 4 sequences,
 21 each block presenting one sequence per condition. Blocks and conditions within blocks were
 22 randomized across participants.
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37 **A Natural face images**

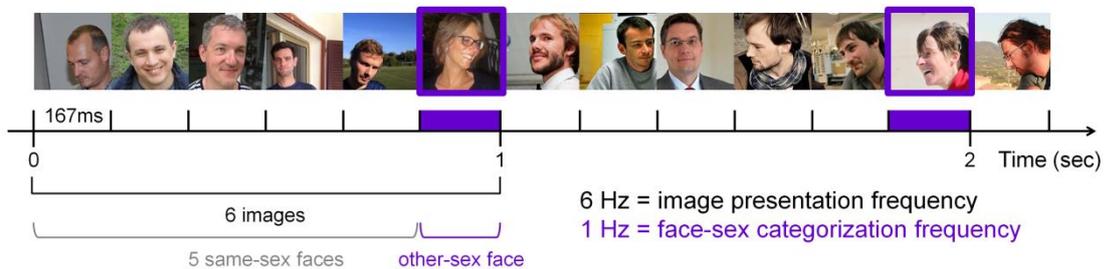
38 Female faces, $N = 33$



39 Male faces, $N = 33$



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 43 **B Face-sex categorization paradigm**



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 51 **Figure 1. Stimuli and Paradigm. A.** Examples of the natural face images used as stimuli. Each picture shows a
 52 male ($N=33$) or female ($N=33$) face unsegmented from its background, with a high degree of within- and between-
 53 sex variability across stimuli, both in terms of image-related (e.g., lighting condition) and person-related (e.g.,
 54 hairstyle) cues. **B.** Face-sex categorization paradigm using fast periodic visual stimulation (FPVS) and a
 55 frequency-tagging approach. The stream of pictures (one sex, here male faces) is presented at a fast 6-Hz base
 56 rate (i.e., 6 pictures / second) with faces of the other sex (here female faces) being inserted every 6th stimulus at a
 57 lower 1-Hz rate (1 change of face sex every second). Two brain responses are thus recorded simultaneously
 58 within one stimulation sequence and can be isolated in the EEG frequency spectrum: a general visual response
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1 (6 Hz and harmonics, i.e. integer multiples) reflecting the processing of all cues rapidly changing 6 times per
2 second (e.g., contrast, face identity), and a face-sex categorization response (1 Hz and harmonics) indexing the
3 discrimination of one sex category from the other and its generalization across individual faces.
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6 After EEG-cap placement, participants were seated in a light- and sound-isolated cabin in
7 front of the screen. Their head was maintained on a chinrest to keep the 57-cm distance to the
8 screen and reduce head movements during testing. Participants were asked to perform an
9 orthogonal task to ensure they maintained their focus on the stimulation during the whole sequence.
10 They were asked to detect a 300 × 300 pixel-large white cross randomly appearing on the images six
11 times per sequence, by pressing the spacebar key using both index fingers simultaneously. Crosses
12 were presented for 200 ms with a minimum 2-second interval between appearances. This task was
13 performed with an average detection rate reaching $99.2 \pm 2.1\%$ (SD) and mean response time for
14 correct detection of 399 ± 39 ms (SD), indicating that participants fully paid attention to the screen
15 during the periodic stimulation.
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24 **2.4. EEG recording and preprocessing**

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26 Scalp electroencephalogram (EEG) was continuously recorded from a 64-channel BioSemi Active-
27 Two amplifier system (BioSemi, The Netherlands) with Ag/AgCl electrodes located according to the
28 10-10 classification system. The Common Mode Sense (CMS) active electrode was used as reference
29 and the Driven Right Leg (DRL) passive electrode was used as ground. EEG analog signal was
30 digitalized at a 1024-Hz sampling rate. During setup, electrode offset was kept between ± 15 μ V for
31 each individual electrode.
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39 EEG analyses were carried out using Letswave 6 (<https://www.letswave.org/>) on Matlab 2017
40 (Mathworks, USA), following a priori procedures validated in previous studies (e.g., Retter and
41 Rossion, 2016). Continuous EEG datasets were first band-pass filtered (cutoff: 0.1 Hz - 100 Hz) using a
42 fourth order butterworth filter, then resampled to 200 Hz. The datasets were then segmented into
43 34-second epochs starting at the beginning of the sequence fade-in (from 2 second before full
44 contrast stimulation to 1 second after the end of fade-out). An Independent Component Analysis
45 (ICA) was computed (e.g., Makeig et al., 1996) to isolate and remove large artifacts generated by eye-
46 blinks (captured by one component in each participant) and additional artifacts over frontal and
47 temporal electrodes (mean number of removed components across participants: 1.4, range: 0–3).
48 Remaining noisy or artifact-ridden electrodes were then linearly interpolated using the 4
49 immediately clean neighboring electrodes (mean number of interpolated electrodes across
50 participants: 1.25, range: 0–6). Epochs were then re-referenced to a common average reference
51 computed using all channels. Following preprocessing, no data were excluded from the analysis.
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2.5. Frequency-domain analysis

Datasets were segmented into 31-second-long epochs, to keep the full-contrast and fade-out recordings of each sequence, thus keeping exactly thirty-one 1-Hz changes of sex (i.e., 6200 time bins). Resulting epochs were averaged per condition to increase the signal-to-noise ratio by reducing the EEG activity non-phase-locked to the stimuli. A fast Fourier transform (FFT) was computed to every averaged epoch and frequency-domain amplitude spectra were extracted for all electrodes with a high frequency resolution of $1/31 \approx 0.0323$ Hz.

Group analysis was first conducted to identify the range of significant harmonics (i.e., target frequencies and integer multiples) to consider in further analysis, for both brain responses. After grand-averaging the FFT spectra across conditions and participants, the 64 channels were pooled together and Z-scores were calculated for each frequency bin as the difference between the signal and the mean noise (i.e., estimated from the 20 surrounding frequency bins, 10 on each side, excluding the immediately adjacent and the 2 most extreme (minimum and maximum) bins) divided by the standard deviation of the noise. Consecutive harmonics were considered significant until Z-scores were no longer greater than 1.64 (i.e., $p < .05$, one-tailed, signal > noise). For the general response, all harmonics reached significance (i.e. 8 harmonics, up to 48 Hz, harmonics were not considered after the 50 Hz response elicited by AC power). For the face-sex categorization response, harmonics were significant until 7 Hz (i.e., 7th harmonic). Then, amplitudes were summed across significant harmonics (Retter and Rossion, 2016) for both responses (excluding the 6th harmonic corresponding to the base frequency (i.e., 6 Hz) for the face-sex categorization response) for each condition and participant, and for every channel. The general visual response and face-sex categorization response will now be referred to these summed responses.

For both brain responses, Z-scores were computed in order to identify the significant channels ($Z > 1.64$, $p < .05$, one-tailed, signal > noise) in grand-averaged data for averaged conditions and each condition separately. Since the whole-scalp power of each response can be high and lead to a significant signal over every channel, amplitude was first normalized for each response (McCarthy and Wood, 1985). This normalization consists in dividing amplitude for each channel by the square root of the sum of the squared amplitude of all channels, thereby allowing the identification of the main electrodes over which the response is largest by scaling differences between electrodes on the global magnitude of the response across the scalp. Finally, based on these significant channels, we defined different regions of interest (ROIs) to be included in statistical analysis. ROIs were separately determined for the general and face-sex responses using the grand-averaged data pooled across all conditions and participants. Three ROIs including middle occipital (mO) and left and right occipito-

1 temporal (IOT and rOT respectively) regions were defined for each brain response (see Results for
2 included channels). Z-scores were also used to identify significant channels in every participant.
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4 To quantify the overall magnitude of each response in a single value expressed in microvolts
5 (μV), non-normalized amplitudes were baseline-corrected by subtracting the mean amplitude of the
6 surrounding noise (same estimation as above). Resulting corrected amplitudes were calculated for
7 every condition and participant, and grand-averaged across participants for illustration purpose.
8 Repeated-measures ANOVAs were run on individual corrected amplitudes for both general and face-
9 sex responses with *Sex of 1-Hz faces* (male, female), *Orientation* (upright, inverted) and *ROI* (IOT, mO,
10 rOT) as within-subject factors, and *Gender of participant* (male, female) as a between-subject factor.
11 Mauchly's test for sphericity violation was performed and Greenhouse-Geisser correction (epsilon: ϵ)
12 for degrees of freedom is reported whenever sphericity was violated. Post-hoc comparisons (Tukey's
13 HSD tests) were conducted for significant effects. Effect sizes are reported as partial eta squared
14 (η_p^2). For visualization of the face-sex categorization response, signal-to-noise ratio (SNR) was also
15 calculated for each channel on the grand-averaged data as the summed amplitude of the response
16 divided by the mean surrounding noise.
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28 **3. Results**

29 **3.1.A neural marker for rapid face-sex categorization**

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31 By inserting faces from one sex every 6 stimuli in a rapid stream of natural face images of the
32 other sex rapidly displayed at 6 Hz, we measured a brain response reflecting single-glance visual
33 categorization of face-sex at exactly 1 Hz (i.e., 6 Hz / 6) and harmonics in the EEG frequency
34 spectrum. Visual inspection of the response summed across significant harmonics and averaged
35 across experimental conditions and participants (Figure 2A) reveals a specific neural signature for
36 face-sex categorization with a magnitude of about 0.3 μV after noise correction. It is mainly recorded
37 over occipito-temporal sites with a right hemisphere advantage. While this response may seem
38 relatively weak, it is clearly identifiable in the amplitude spectrum at both the group and individual
39 participants levels (Figure 2D), with a mean signal-to-noise ratio (SNR) of ≈ 1.17 (i.e., 17% of signal
40 increase). A complementary analysis conducted during the first and last 6 seconds (out of 31) of
41 stimulation revealed that the face-sex categorization response rapidly emerges during the fast train
42 of individual faces and remains of comparable amplitude at the end of the sequence (Supplementary
43 Information and Figure S3).
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56 We assessed whether the face-sex categorization response averaged across conditions is
57 significantly larger than the noise using Z-scores. We found a significant response ($Z > 1.64$, $p < .05$,
58 one-tailed, signal > noise) over 12 channels (range: $1.76 < Z < 10.24$) located in posterior regions (i.e.,
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P6, P7/8, P9/10, PO4, PO7/8, O1/2, Oz, Iz) and over only one central channel (C1, $Z = 2.83$) for the group. Thanks to the high SNR of the approach, we also calculated Z-scores for each individual participant. Thirty out of 32 participants showed a significant response over at least one of the 12 posterior channels identified for the group (Figure 2B), with a mean number of 4 ± 2.5 (SD) significant channels (range: 1–10). Scalp-wide analysis revealed that for the two remaining participants, one had a significant response over 4 channels while no channels reached significance for the other participant. Inspection of individual topographical maps (Figure 2C) shows clear face-sex categorization responses and a right-hemispheric dominance in most participants.

A significant response was also evidenced in each condition separately (Figure 3A for topographical maps per condition). At the group level, the male upright and inverted condition respectively yielded significant responses over 6 and 7 out of the 12 channels previously identified for all conditions combined. Similarly, 10 out of the 12 electrodes were significant for upright female faces and 7 channels for inverted female faces. At the individual level, a large proportion of participants showed a response for each condition when considering those 12 channels (between 27 and 31 out of 32 participants per condition). Individually, those participants showed between 1 and 8 out of 12 channels presenting a significant face-sex categorization response.

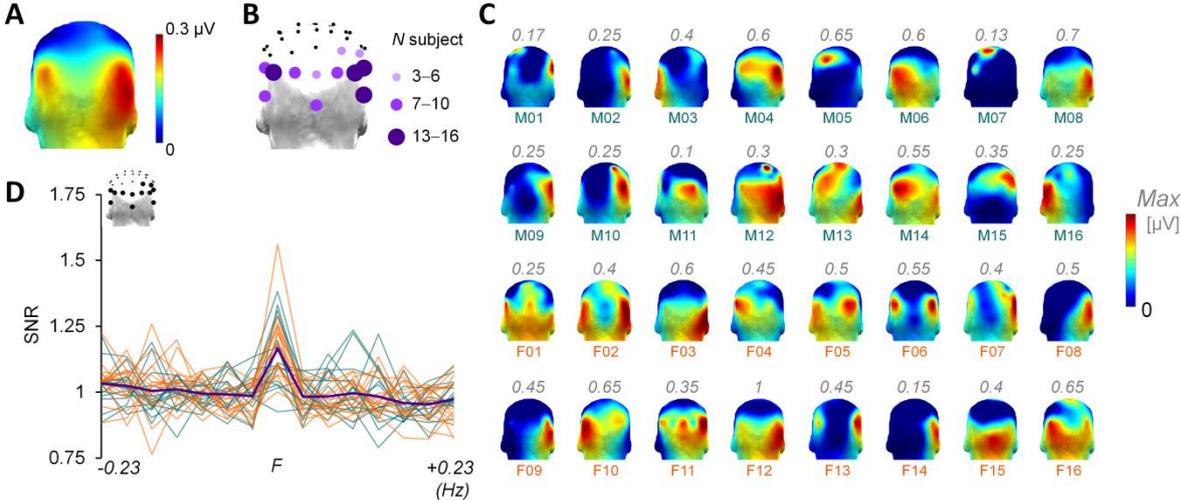


Figure 2. The face-sex categorization response. **A.** Topographical map (back view) of the face-sex categorization response (expressed in baseline-corrected amplitudes summed across significant harmonics; i.e., 1 Hz and integer multiples) averaged across conditions and participants. The response is located over occipito-temporal regions, with a right hemisphere advantage. **B.** Number of participants (indicated by circle size) showing a significant face-sex categorization response averaged across conditions for each posterior channel among the 12 significantly responding at the group level (see text for details). **C.** Individual topographical maps (back view) of the face-sex categorization response pooled across conditions. Each individual color scale ranges from 0 to its maximal amplitude indicated by the grey value above its corresponding map. **D.** Signal-to-noise ratio (SNR) of the face-sex categorization response summed across harmonics (F) and averaged across conditions and responding channels. The bold purple line represents group data while orange and turquoise lines respectively represent female and male participants. EEG frequency spectrum is depicted from -0.23 Hz to $+0.23$ Hz around F , showing a clearly identifiable face-sex categorization response (mean SNR ≈ 1.17 , 17% of signal increase).

3.2. Asymmetrical pattern of response between upright male and female faces

According to the channels showing a significant face-sex categorization response across conditions and participants, the following analysis considered three ROIs. The middle occipital region (mO) gathered Oz, Iz, O1 and O2. The left and right occipito-temporal regions (lOT and rOT respectively) averaged P9/10, P7/8, PO7/8, P5/6 and PO3/4, thus adding P5 ($Z = -0.52$) and PO3 ($Z = -0.18$) to the aforementioned 12 significant channels to include homologous channels across hemispheres.

As illustrated in Figure 3A, the main effects of *Sex of 1-Hz faces* ($F(1, 30) = 7.33$; $p = .01$; $\eta_p^2 = 0.20$) and *Orientation* ($F(1, 30) = 8.42$; $p = .007$; $\eta_p^2 = 0.22$) were qualified by a significant interaction ($F(1, 30) = 5.72$; $p = .02$; $\eta_p^2 = 0.16$) indicating that in the upright orientation, female faces among male faces elicit a larger response (mean \pm SEM: $0.3 \pm 0.04 \mu\text{V}$) than male faces among female faces ($0.13 \pm 0.03 \mu\text{V}$; $p < .001$). This difference was no longer found for inverted images, as the response to female faces ($0.17 \pm 0.04 \mu\text{V}$) does not differ significantly from the response to male faces ($0.13 \pm 0.03 \mu\text{V}$; $p = .77$). Accordingly, there was a significant difference between upright and inverted orientations only for female faces (43% decrease, $p = .007$; male faces: $p = .99$). A marginally significant effect of *ROI* ($F(2, 60) = 2.99$, $p = .06$; $\eta_p^2 = 0.09$) revealed a trend for the right hemisphere dominance (lOT: $0.16 \pm 0.03 \mu\text{V}$; mO: $0.18 \pm 0.03 \mu\text{V}$ and rOT: $0.22 \pm 0.02 \mu\text{V}$; $p = .057$ and $p = .19$ respectively for rOT vs. lOT and rOT vs. mO) visible on the topographical map (Figure 2A). No other significant effects or interactions were found for the face-sex categorization response. In particular, neither the main effect of *Gender of participant* ($F(1, 30) = 2.19$; $p = .15$; $\eta_p^2 = 0.07$) nor its interaction with other factors reached significance ($ps > .10$).

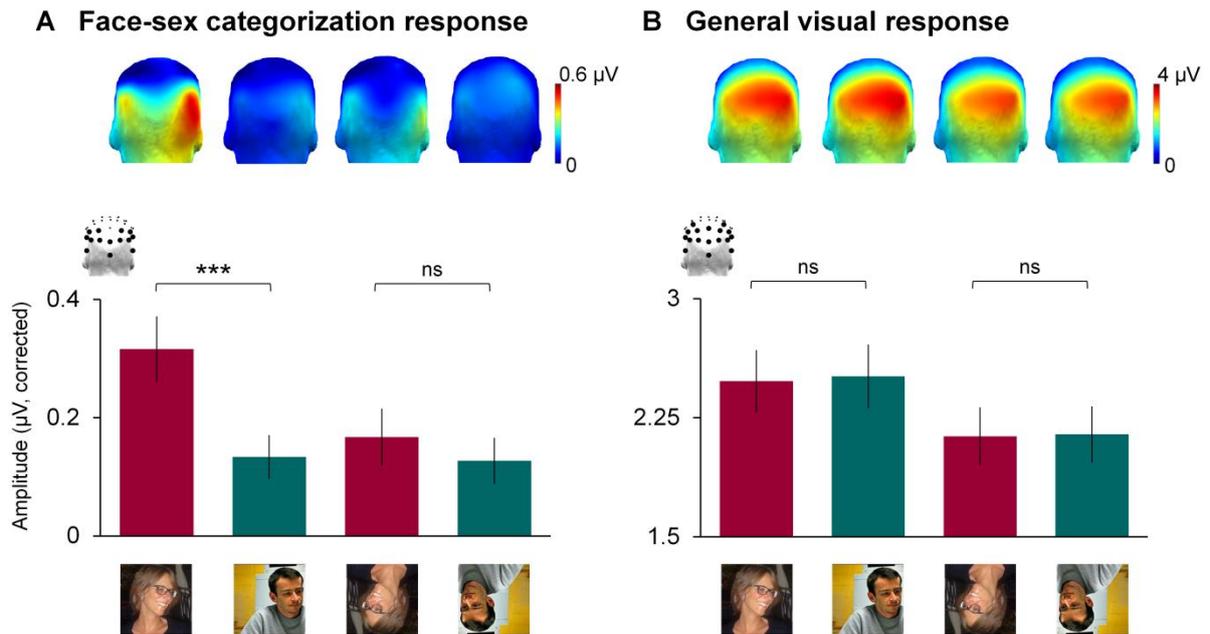


Figure 3. Face-sex categorization and general visual responses across conditions. **A.** Topographical maps (back view) of the face-sex categorization response along with its summed baseline-corrected amplitude averaged across regions-of-interest (ROIs) for each condition (error bars represent standard error of the mean). For the upright orientation, female faces presented among male faces elicit a larger response than the reverse. This difference is no longer significant for the inverted orientation (***) $p < 0.001$; ns $p > 0.05$). **B.** Topographical maps (back view) of the general visual response along with its mean baseline-corrected amplitude across ROIs for each condition. The general visual response is significantly diminished for upside-down face images (see text for details) but it is not modulated by the sex of the 1-Hz faces.

3.3. General visual processes elicited by all face images

The brain response recorded at the rapid 6-Hz base rate of stimulation and its harmonics reflects general visual processes elicited by all face images, with the contribution of both low- (e.g., contrast) and higher-level (e.g., face identity) cues rapidly changing 6 times per second. Averaged across conditions, Z-scores showed a significant response for 13 channels (P4, P6, P8, P10, PO7/8, PO3/4, O1/2, Oz, Iz, and POz) at group level, and every participant showed a significant response for at least 7 out of those 13 channels. Furthermore, all participants had a significant response for the middle occipital electrode Iz. When considering each condition separately, the general visual response is significant over the same electrodes and one or two additional electrodes depending on the condition. As for the face-sex categorization response, visual inspection reveals a right-hemispheric dominance, but with a more middle occipital topography (Figure 3B).

Based on the 13 significant channels, three ROIs were defined. The middle occipital region (mO) gathered POz, Oz, Iz, O1 and O2. The left and right occipito-temporal regions (lOT and rOT respectively) were composed of P9/10, P7/8, P5/6, P3/4, PO7/8 and PO3/4, thus adding symmetrical channels in order to even ROIs. The repeated-measures ANOVA revealed a main effect of ROI ($F(1.7, 49.5) = 33.47$; $\epsilon = 0.83$; $p < .001$; $\eta_p^2 = 0.53$) with a larger response over mO ($2.97 \pm 0.2 \mu\text{V}$) than rOT

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($2.28 \pm 0.16 \mu\text{V}$; $p < .001$) and IOT ($1.70 \pm 0.1 \mu\text{V}$; $p < .001$). The two latter regions also significantly differ ($p = .001$). The main effect of *Orientation* ($F(1, 30) = 26.9$; $p < .001$; $\eta_p^2 = 0.47$) showed that inverted images ($2.14 \pm 0.12 \mu\text{V}$) elicit a lower response (14% decrease) than upright ones ($2.5 \pm 0.15 \mu\text{V}$), as visible in Figure 3B. An additional effect of *Gender of participant* ($F(1, 30) = 5.06$; $p = .03$; $\eta_p^2 = 0.14$) was found with a larger mean response in female ($2.60 \pm 0.19 \mu\text{V}$) than in male ($2.04 \pm 0.16 \mu\text{V}$) participants. Importantly for our purpose, no significant effect of *Sex of 1-Hz faces* ($F(1, 30) = 0.40$; $p = .53$; $\eta_p^2 = 0.01$) nor its interactions with other factors ($ps > .35$) were found for the general visual response.

4. Discussion

Using FPVS-EEG with faces from one sex periodically (i.e., at 1 Hz) interspersed among faces from the other sex, we objectively (i.e., at pre-experimentally defined frequencies) isolated and quantified a direct (i.e., without post-hoc subtraction) brain response selective to face sex over occipito-temporal regions with a right hemisphere advantage. This response is elicited automatically (i.e., participants did not explicitly judge face sex) and at a single glance in the fast 6-Hz train of stimuli (≈ 167 ms per stimulus). Moreover, thanks to forward- and backward-masking of the stimuli and a non-periodic orthogonal task, the face-sex categorization response is free from decisional and motor processes. Importantly, the response is a signature of high-level visual categorization of face sex reflecting the discrimination between face sexes generalized across face images despite variable exposure conditions (e.g., lighting) and physiognomic features (e.g., hairstyle). In addition, despite a relatively low EEG amplitude ($\approx 0.3 \mu\text{V}$), the face-sex categorization response is clearly identifiable in the EEG frequency spectrum (17% larger than surrounding noise), already identifiable from the first 6 seconds of stimulation (Supplementary Information and Figure S3), and significant in most individual participants. This is not a trivial achievement considering the weak and inconsistent effects reported by previous EEG studies (Carrito et al., 2018; Cellerino et al., 2007; Dickter and Bartholow, 2007; Ito and Urland, 2005, 2003; Kecskes-Kovacs et al., 2013; Kloth et al., 2010; Kovács et al., 2006; Mouchetant-Rostaing et al., 2000; 2003; Rakić et al., 2018; Sun et al., 2010; Yokoyama et al., 2014; Zhang et al., 2016). We attribute the robustness of the face-sex categorization response found here to four factors. First, rather than homogenized stimuli, we used natural images with all potential cues for sex categorization. Second, rather than using an indirect comparison of two responses dominated by low-level inputs (i.e., elicited by faces appearing after a uniform background), we directly measure a *contrast* between male and female faces in this paradigm. Third, we take advantage of the high sensitivity of the FPVS-EEG approach, in which the response of interest projects to small predefined bins of the frequency spectrum associated with little noise (Regan, 1989; Rossion, 2014). Finally, any distinct brain response to a change of face sex (i.e., enhanced, reduced, shifted in time, differing in

1 shape) is captured with frequency-domain representation, increasing the ability to reliably identify
2 sex-selective neural activity in every individual participant even in case of high between-subject
3 variability.
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6 Although the brain response reported here reflects generalized face-sex categorization
7 across highly variable images, it does not mean that various diagnostic cues for sex recognition do
8 not contribute to the response. Previous research indeed showed that shape information (Brown and
9 Perrett, 1993; Roberts and Bruce, 1988; Yamaguchi et al., 1995) and skin color, texture or contrast
10 (Dupuis-Roy et al., 2018, 2009; Nestor and Tarr, 2008; Russell, 2003, 2005) are important cues for
11 face sex identification, both locally (i.e., for isolated features) and globally (i.e., across the whole face,
12 Baudouin and Humphreys, 2006; Brown and Perrett, 1993; Burton et al., 1993; Yamaguchi et al.,
13 1995; Zhao and Hayward, 2010). For instance, the overall sharp shape (i.e., angular chin and jaws +
14 protuberant nose + salient eyebrows; Roberts and Bruce, 1988) or the redder skin color (Dupuis-Roy
15 et al., 2009; Nestor and Tarr, 2008) generally associated with male faces may strongly contribute to
16 sex-selective neural activity. In addition, some other cues typically associated with sex and generally
17 controlled by elimination or homogenization in experimental settings (e.g., hairstyle, beard, make-
18 up, jewelry) were not removed from the natural images used in the present study. As an illustration,
19 we estimated which cues may have contributed to the response by comparing how frequently those
20 cues are present in the two sets of male and female faces (Table S1). Hair length, cosmetic/jewelry,
21 baldness and facial hair all significantly differ between males and females whereas glasses, facial
22 expression and viewpoint do not. The former cues could thus account for the emergence of the sex-
23 selective response. Besides, we observed a diminished sex-selective response with picture-plane
24 inversion, in line with previous evidence indicating a reduced ability to identify face sex in inverted
25 faces (Bruce and Langton, 1994; Burton et al., 1993; Reddy et al., 2004; Zhao and Hayward, 2010).
26 Since inversion particularly disrupts holistic perception – i.e. the automatic integration of facial cues
27 into a unified representation (Rossion, 2009, 2008 for reviews; Tanaka and Farah, 1993), this
28 suggests that relationships between features, rather than only local features, were also diagnostic for
29 sex categorization. These different sex-selective cues can thus lead to a common high-level neural
30 categorization response at each change of face sex.
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51 An interesting finding of the present study is the larger response to female faces among male
52 faces than to male faces among female faces. Since this asymmetry was only observed for upright
53 faces, the contribution of low-level physical variability across images (e.g., more variable low-level
54 visual cues for one stimulus set) is unlikely. Rather, in our sample of images at least, females could
55 form a more homogenous category than males due to greater similarity across individual female
56 faces facilitating generalization across the exemplars appearing at the 1 Hz periodic rate. This high
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generalizability may be particularly driven by the whole face configuration since the sex-selective response to female among male faces is reduced by picture-plane inversion. In contrast, the similar response observed in both orientations for males among females suggests that male categorization relies more on local sex-selective cues. Previous studies have shown that female faces are generally rated as more typical (i.e., closer to the average face; Vokey and Read, 1992) and attractive (Hume and Montgomerie, 2001; Vokey and Read, 1992) than male faces, both measures being associated with lower variability between individuals (O'Toole et al., 1994). Overall, these findings are related to sexual selection of more attractive females than males (e.g., Darwin, 1981; Symons, 1987). This higher attractiveness (and lower variability) is strengthened by the use of cosmetics and other forms of facial elaboration, at least for Caucasian faces such as those used in the present study (Alley and Hildebrandt, 1988). However, it is worth noting that cosmetics and jewelry are not systematically present in our set of female images (Figure S1 and Table S1).

The reverse interpretation could also be true, given that the face-sex categorization response is not an absolute mean response to faces from one sex contrasted to a blank baseline, but a direct differential response to faces from one sex contrasted to faces from the other sex. Therefore, the amplitude of the response depends on how both male and female faces are processed. Accordingly, if male faces shared larger similarity and higher generalizability within a well-defined category that excludes most female faces, the discrimination of each female face following 5 male faces in the stimulation sequence would be stronger. The whole male face configuration could trigger this high generalizability leading to a larger response to female among male faces in the upright compared to inverted orientation. In contrast, female faces could be categorized more from local facial features, leading to a sex-selective response to males among females of similar magnitude in both orientations. Previous studies indeed found that female faces are classified more slowly (O'Toole et al., 1998) and/or less accurately (Bruce and Langton, 1994) than male faces. These observations support the idea that female faces could be more dissimilar and constitute a less homogeneous category than male faces. In addition, sex classification of male faces resists stronger degradation by Gaussian noise filtering or pixelation than female faces (Cellerino et al., 2004), suggesting a more efficient perception of a male face, relying on the overall face shape even when features are strongly degraded and unidentifiable. One could argue that those findings were observed using edited homogenous stimuli (e.g., hairless) which bias the categorization of female faces as males. However, in a side experiment, we also found that female faces are judged more slowly (but as accurately) than male faces with our own set of unedited images (Supplementary information & Table S2). In sum, reviewed evidence is mixed and does not favor any interpretation. While our own data suggest that male faces, at least in the Caucasian sample tested here, may constitute a homogenous category

1 while the female face category is broader and includes more dissimilar exemplars, further studies
2 should be conducted to explore those possible accounts of the asymmetric categorization of female
3 vs. male faces, for instance testing whether it generalizes to other sets of face images (e.g., Asian or
4 African faces).
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7 One could also underline that face-sex categorization takes less than the 1-second interval
8 between two changes of face sex, and that further sex-related processes are captured by the sex-
9 selective response (provided that they co-occur with the periodic changes of face sex once every
10 second). This could be a non-exclusive potential factor of the asymmetry. For instance, face sex is
11 reliably associated with social attributes, the most feminine faces being perceived as more
12 trustworthy (e.g., Oosterhof and Todorov, 2008), happier (e.g., Hess et al., 2009) or less dominant
13 (e.g., Boothroyd et al., 2007). Future studies should explore the possible contribution of such sex-
14 related processes. Nonetheless, since a process that reliably co-occurs with a change face sex is, in
15 fact, an integral part of what differentiates male and female face categories, this point highlights that
16 the neural response we measured is a full neural signature of face-sex categorization, reflecting the
17 contribution of any process related to a change of face sex.
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21 It is noteworthy that we did not find different face-sex categorization responses according to
22 the gender of participants. An own-gender bias has been often reported in the literature, as a better
23 performance to process own-gender faces. However, it is consistently observed during individual
24 face recognition tasks (for a meta-analytic review, see Herlitz and Lovén, 2013), but not generally
25 found during explicit face-sex judgments (e.g., Dupuis-Roy et al., 2009; but see Yamaguchi et al.,
26 1995). The only difference we observed depending on the gender of participants was a larger middle
27 occipital response to the stream of stimulation in females. On a side note, this general response to all
28 face images was also lower for upside-down than upright faces, in accordance with previous
29 evidence (Liu-Shuang et al., 2014; Zimmermann et al., 2019). More specifically, by using rapid 6-Hz
30 streams of natural face images to isolate familiar face identity recognition in the brain, Zimmerman
31 and collaborators (2019) found an inversion effect of identical magnitude (14% decrease). Given that
32 face identity changes 6 times per second in both studies, reduced neural activity in response to a fast
33 train of upside-down individual faces may be partly due to impaired face individuation following
34 picture-plane inversion (i.e., faces are perceived as being more similar to one another when
35 appearing upside-down, leading to increased adaptation effects of face repetition, see Rossion et al.,
36 2012). Additionally, the general visual response was not modulated by face sex, emphasizing its
37 dissociation from the face-sex categorization response of interest.
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One limitation of the present study may come from the use of the same number of male and female face images in every condition ($N = 33$). When images from one sex were presented as base stimuli, all 33 exemplars were first randomly displayed before a new draw was made from the same images. As a consequence, the base stimuli were repeated 5 times for each 33-sec stimulation sequence, while stimuli interleaved in between to change face sex were only presented once. Nevertheless, stimulus repetition started only after 6.5 seconds of stimulation whereas the face-sex categorization response is already significant during the first 6 seconds of stimulation (Supplementary Information and Figure S3). Moreover, responses recorded during the first and last 6 seconds of stimulation are of comparable amplitude, suggesting that sex-selective neural activity is stable throughout the whole stimulation sequence. Hence, the neural response isolated here is not due or modulated by this repetition factor and appears to be a valid signature of face-sex categorization in the human brain.

Altogether, the present findings reveal that rapid and automatic face-sex categorization from natural images can be objectively isolated and quantified in the human brain within a few minutes. This sex-selective response reflects categorization of face sex (i.e., discrimination between the two sexes and generalization across faces from one sex) invariant to physical changes (i.e., across exposure conditions) and physiognomic differences (i.e., across individual faces). The response is robust at group and individual levels. Such a sensitive neural marker could therefore be used in future studies to investigate more precisely the nature of sex categorization mechanisms in the human brain, and more generally to characterize sex-selective processing in any population who cannot provide explicit judgment of face sex (e.g., infants).

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Declaration of interest

None.

Supplementary data

EEG, behavioral data and experiment code associated with this article (from main and supplementary analyses) are freely available at <http://dx.doi.org/10.17632/p3zzk5kmc6.1>.

Legal copyright restrictions prevent us from publicly archiving the face stimuli online. Readers seeking access to the images for research should contact the senior author (arnaud.leleu@u-bourgogne.fr). Access will be granted to named individuals who complete a formal agreement stating that images will only be used for research.

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A Natural face images

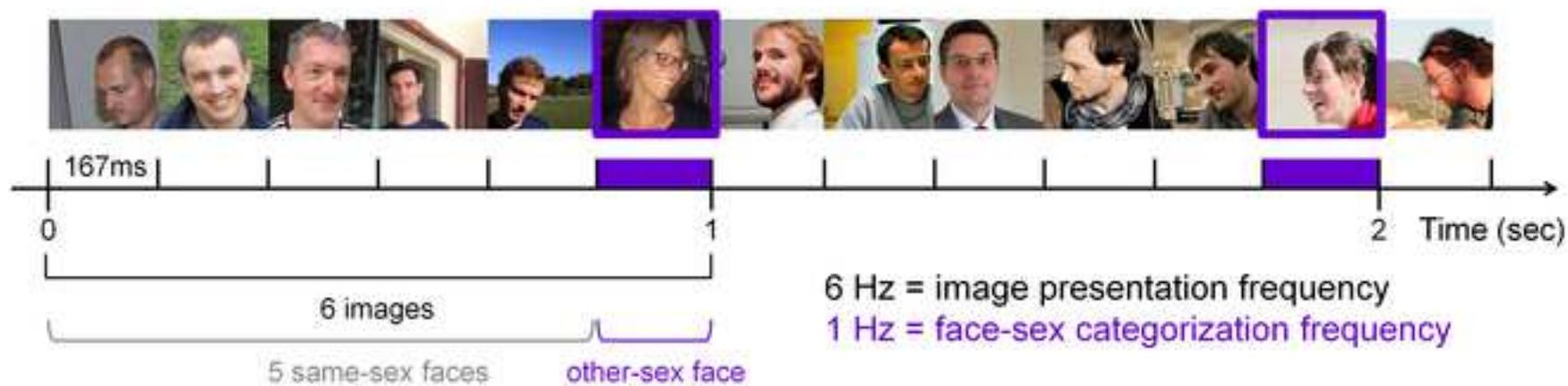
Female faces, $N = 33$

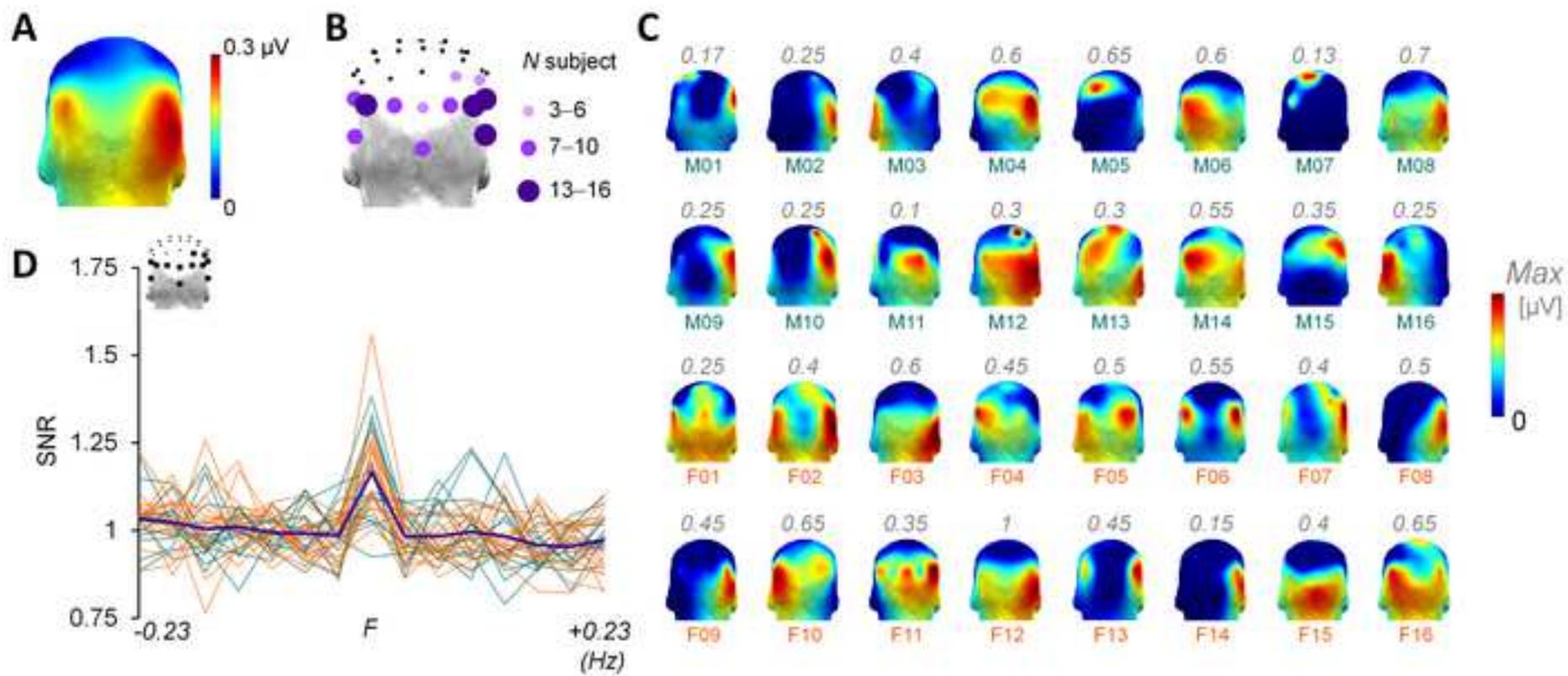


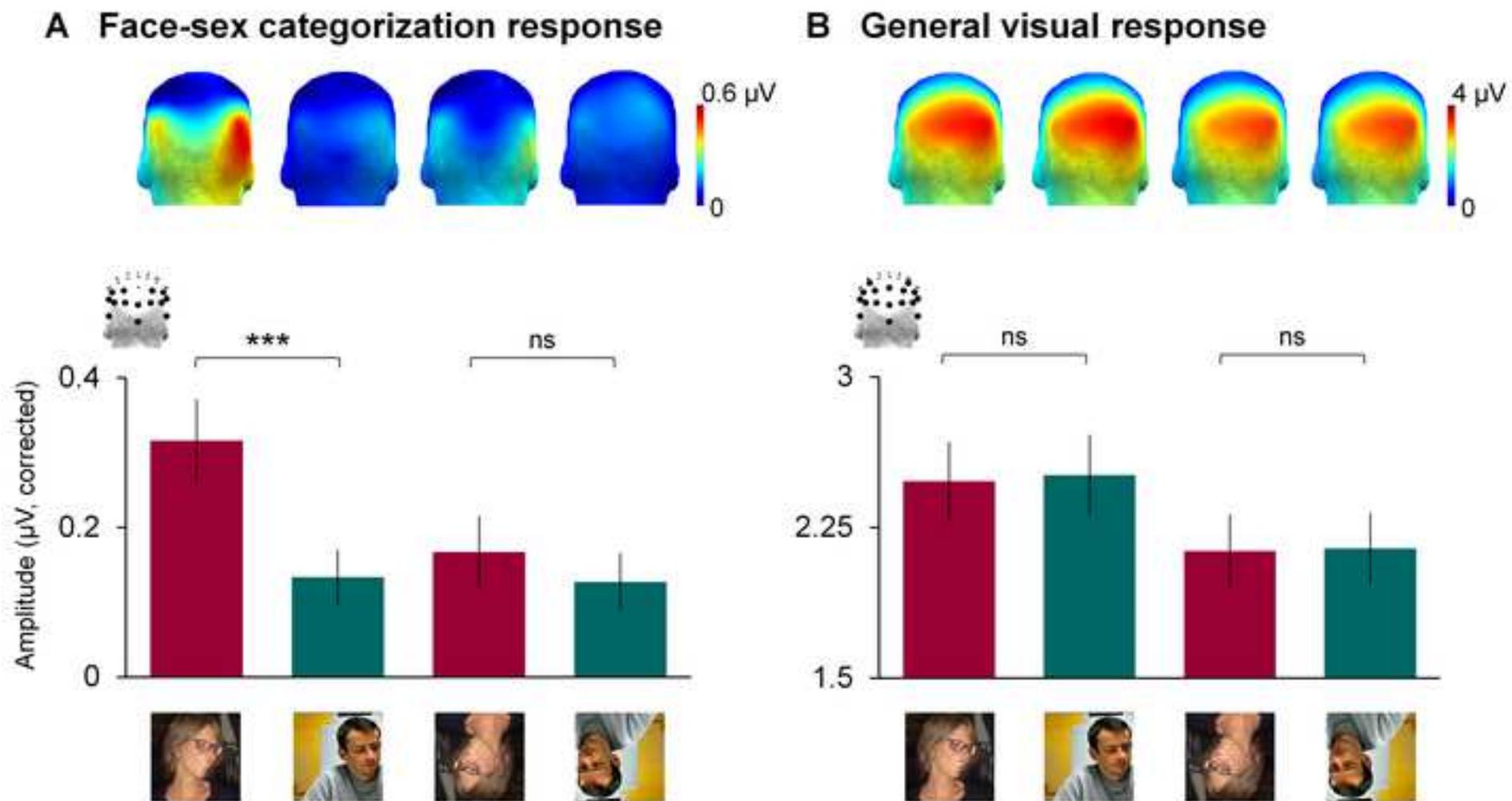
Male faces, $N = 33$



B Face-sex categorization paradigm









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