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## Fast Periodic Auditory Stimulation Reveals a Robust Categorical Response to Voices in the Human Brain

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1 **Manuscript Title Page**

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4 voices in the human brain

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7

8 **3. Authors Names and Affiliations:**

9 Francesca M. Barbero<sup>1</sup>, Roberta P. Calce<sup>1</sup>, Siddharth Talwar<sup>1</sup>, Bruno Rossion<sup>1,2,3</sup>, Olivier Collignon<sup>1,4</sup>

10 <sup>1</sup>Institute of Research in Psychology (IPSY) & Institute of Neuroscience (IoNS), Louvain Bionics Center,  
11 University of Louvain (UCLouvain), 1348 Louvain-la-Neuve, Belgium

12 <sup>2</sup>Université de Lorraine, CNRS, CRAN, F-54000 Nancy, France

13 <sup>3</sup>Université de Lorraine, CHRU-Nancy, Service de Neurologie, F-54000, France

14 <sup>4</sup>Center for Mind/Brain Sciences (CIMeC), University of Trento, 38068 Rovereto, Italy

15

16 **4. Authors Contributions:** FMB, OC and BR designed research; FMB and RPC performed research; FMB,  
17 RPC and ST analyzed data; FMB, OC and BR wrote the paper.

18

19 **5. Correspondence should be addressed to:** Francesca M. Barbero (francesca.barbero@uclouvain.be) and  
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47 **Abstract**

48 Voices are arguably among the most relevant sounds in humans’ everyday life, and several studies have  
49 suggested the existence of voice-selective regions in the human brain. Despite two decades of research,  
50 defining the human brain regions supporting voice recognition remains challenging. Moreover, whether  
51 neural selectivity to voices is merely driven by acoustic properties specific to human voices (e.g.  
52 spectrogram, harmonicity), or whether it also reflects a higher-level categorization response is still under  
53 debate. Here, we objectively measured rapid automatic categorization responses to human voices with

54 Fast Periodic Auditory Stimulation (FPAS) combined with electroencephalography (EEG). Participants were  
55 tested with stimulation sequences containing heterogeneous non-vocal sounds from different categories  
56 presented at 4 Hz (i.e., 4 stimuli/second), with vocal sounds appearing every 3 stimuli (1.333 Hz). A few  
57 minutes of stimulation are sufficient to elicit robust 1.333 Hz voice-selective focal brain responses over  
58 superior temporal regions of individual participants. This response is virtually absent for sequences using  
59 frequency-scrambled sounds, but is clearly observed when voices are presented among sounds from  
60 musical instruments matched for pitch and harmonicity-to-noise ratio. Overall, our FPAS paradigm  
61 demonstrates that the human brain seamlessly categorizes human voices when compared to other sounds  
62 including matched musical instruments and that voice-selective responses are at least partially  
63 independent from low-level acoustic features, making it a powerful and versatile tool to understand human  
64 auditory categorization in general.

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#### 67 **Significance statement**

68 Voices are arguably among the most relevant sounds we hear in our everyday life, and several studies have  
69 corroborated the existence of regions in the human brain that respond preferentially to voices. However,  
70 whether this preference is driven by specific acoustic properties of voices or if it rather reflects a higher-  
71 level categorization response to voices is still under debate. We propose a new approach to objectively  
72 identify rapid automatic voice-selective responses with frequency tagging and electroencephalographic  
73 recordings. In four minutes of recording only, we recorded robust voice-selective responses independent  
74 from low-level acoustic cues, making this approach highly promising for studying auditory perception in  
75 children and clinical populations.

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## 1. Introduction

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Voices of conspecifics are arguably among the most relevant sounds we hear in our everyday life: they do not only carry speech, but also convey a wealth of information about the speakers such as their sex, age, emotional status, identity, trustworthiness, etc. (Belin et al., 2004). Regions in the human brain located along the bilateral superior temporal sulcus (STS) respond more to human voices than to other sounds (“Temporal Voice Areas”, TVAs), playing a key role in voice recognition (Belin et al., 2002, 2000). However, whether this selectivity is fully accounted for by specific acoustic properties of voices (Moerel et al., 2012; Ogg et al., 2019; Staeren et al., 2009), or if it also reflects a higher-level categorization response beyond these low-level auditory properties is still under debate. This question has been previously addressed through careful choice and design of acoustic stimuli (Agus et al., 2017; Belin et al., 2002; Levy et al., 2003) and sophisticated signal analyses (Moerel et al. 2012; Giordano et al. 2013; Leaver & Rauschecker 2010), with results sometimes challenging the notion of brain regions dedicated to the abstract encoding of voices (Ogg et al., 2019; Santoro et al., 2017). For instance, regions identified as voice-selective present a response bias to low frequencies typical of voices, even when responding to tones (Moerel et al., 2012),

108 and portions of auditory cortex are sensitive to the degree of harmonic structure present in both artificial  
109 sounds and in human vocalizations (Lewis et al., 2009).

110 The approaches used so far to delineate voice-selectivity in the human brain, mostly relying on  
111 functional Magnetic Resonance Imaging (fMRI) or event-related potential recordings with  
112 electroencephalography (EEG), present limitations that hinder the characterization of a putative high-level  
113 voice-categorization response. For instance, these methods usually imply the subtraction between neural  
114 responses elicited by voices and control sounds which occurred at different times, or the regression of  
115 parameters linked to low-level properties of sounds, when in fact the subtracted components might be a  
116 part of the expression of a response to voices (Frühholz and Belin, 2018).

117 Here we shed light on the nature of voice-selective responses in the human brain by proposing a  
118 new approach to identify these automatic responses objectively and directly (i.e. without  
119 subtraction/regression). This approach relies on electroencephalographic recordings and, more specifically,  
120 on “EEG frequency tagging” (Regan 1989). Frequency tagging builds on the principles of so-called steady-  
121 state evoked responses: under periodic external stimulation, the brain region encoding that input responds  
122 at the exact same stimulation frequency (Norcia, Appelbaum, Ales, Cottareau, & Rossion, 2015 for review).  
123 We developed a Fast Periodic Auditory Stimulation (FPAS) paradigm adapted from studies in vision, in  
124 particular to study face (Retter and Rossion, 2016; Rossion et al., 2015) and letter/word categorization  
125 (Lochy et al., 2015). Specifically, participants listened to sequences of heterogeneous sounds presented at a  
126 periodic rate of 4 Hz. Critically, each third sound presented in the sequences was a (different) human voice  
127 excerpt, so that voices were presented at a periodic rate of 1.333 Hz. In the EEG frequency domain, a  
128 response at the sound presentation frequency would reflect shared processes between all sounds, while a  
129 putative activity at the voice presentation rate would emerge only if the participant’s brain successfully  
130 *discriminates* human voices from other sounds and *generalizes* across all the diverse vocal samples  
131 presented (to maintain periodicity). To further assess whether low-level properties alone could elicit voice-  
132 selective responses, we included a second stimulation sequence with identical periodicity constraints using  
133 the same sounds but frequency-bins scrambled (Dormal et al., 2018) to preserve the overall frequency  
134 content of the original sounds while disrupting their harmonicity and intelligibility. In a second experiment,

135 we implemented a sequence presenting voices among musical instrument notes that were matched for  
136 pitch, harmonicity-to-noise ratio (HNR) and spectral center of gravity to control for frequency content of  
137 the sounds, harmonicity and within category homogeneity (Belin et al., 2011, 2002).

138 In summary, the goal of the present study was both conceptual and methodological. We aimed to  
139 develop a FPAS paradigm combined with EEG to test whether and to which extent voice-selective  
140 responses are partially independent from low-level acoustic features. Since FPAS provides a marker for  
141 categorization that is objective, direct and does not require overt responses to voices from the participants,  
142 we expect our observations to hold significant value for further characterization of the nature of voice-  
143 selectivity in the human brain.

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## 145 **2. Materials and methods**

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### 147 **2.1 Experiment 1 – Voice versus object sounds**

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#### 149 **2.1.1 Participants**

150 EEG was recorded in twenty participants (age range 19-26 years, 10 female) in experiment 1. Data  
151 from four participants were excluded due to the presence of EEG artefacts. All participants were right-  
152 handed and reported normal or corrected to normal vision, normal hearing and no history of psychiatric or  
153 neurological disorders. The experiment was approved by the local ethical committee of the University of  
154 Louvain (Project 2016-25); all participants provided written informed consent and received financial  
155 compensation for their participation.

#### 156 **2.1.2 Stimuli**

157 Individual sounds used to create the *standard sequences* were 250 ms long, leading to a base  
158 stimulation frequency of 4 Hz (1/250ms) and a target frequency of 1.333 Hz (4Hz/3: vocal stimuli presented  
159 each third sound) and were selected in an effort to be as heterogeneous and variable as possible. We  
160 selected 137 non-vocal stimuli including environmental sounds (e.g. water pouring, rain), musical  
161 instruments, sounds produced by manipulable and non-manipulable objects (e.g. telephone ringing,

162 ambulance siren). We selected 55 vocal stimuli including speech and non-speech vocalizations pronounced  
163 by speakers of different sex, age and emotional states. Stimuli were extracted from various sources  
164 including online databases, extracts from audiobooks and the Montreal Affective Voices dataset (Belin et  
165 al., 2008). These stimuli were then frequency scrambled using the method described in Dormal et al. 2018  
166 to create the *scrambled sequences*. Specifically, we applied a fast Fourier transformation to vocal and non-  
167 vocal sounds and created frequency bins of 200 Hz. Within each of these frequency windows, we shuffled  
168 the magnitude and phase of each Fourier component. We then performed an inverse Fourier transform to  
169 the signal and then applied the original sound envelope to the scrambled sound. As a result, the scrambled  
170 sounds have frequency content and spectral-temporal structure (change of energy of some frequencies  
171 over time) that are almost identical to that of the original stimuli (Figure 1C). However, the harmonicity is  
172 altered and the intelligibility of the stimuli is disrupted as confirmed by the behavioral experiment  
173 (experiment 3, Figure 5). All sounds were equalized in overall energy (RMS) and faded-in and -out with 10  
174 ms ramps in order to facilitate individual sounds segregation and avoid clicking.

### 175 **2.1.3 Procedure**

176 A schematic representation of the experimental design is shown in Figure 1B. Sounds of the same  
177 duration were presented one after another to create periodic auditory sequences. In particular, sounds  
178 were presented such that each third sound was a human voice. Vocal and non-vocal samples were selected  
179 from various sources and were as heterogeneous as possible to represent the variability characteristic of a  
180 sound category (and thus also naturally increasing the variability of low-level acoustic features). No  
181 auditory category other than voice was presented periodically. Participants listened to two different  
182 sequence types that were created to measure voice selectivity using naturalistic stimuli (*standard*  
183 *sequence*) and to control for low-level acoustic confounds (i.e. frequency content, *scrambled sequences*). If,  
184 at the target (voice) rate, the standard and the scrambled sequences evoke responses that are  
185 quantitatively (amplitude of the response) and qualitatively (topographical map, pattern of harmonics)  
186 similar, it would indicate that we are interpreting as voice-selective responses that are elicited by frequency  
187 content alone. Each stimulation sequence was 64 s long, including 2 s of fade-in and -out during which the  
188 presentation volume raised gradually from 0 to the maximum at the start of the sequence, and vice versa

189 at the end of the sequence. Fading-in and –out were introduced to avoid abrupt movements that the  
190 sudden onset of the sequences could have provoked and that would have introduced artefacts in the data.  
191 Sequences for both conditions were presented four times in a pseudorandomized order. Individual  
192 sequences with a new pseudo-randomized order of stimulus presentation were generated before testing  
193 for each repetition and for each individual participant in an effort to increase generalization; all sequences  
194 played during the testing therefore constitute unique exemplars that share presentation parameters (base  
195 and target frequencies) and the sounds which were used to build them, but systematically presenting them  
196 in different orders in each sequence and each participant. During testing, participants were asked to  
197 perform an orthogonal non-periodic task: they had to press a button whenever they heard a sound that  
198 was presented at a lower volume as compared to the volume of the other sounds in the sequence. Volume  
199 reduction was obtained by decreasing the sounds' root mean square values of a factor of 12.5. Each  
200 sequence contained six attentional targets (including both vocal and non-vocal sounds) that were  
201 introduced in a pseudorandomized order (excluding fade-in and -out period at the start of the sequence).  
202 Participants were required to listen to the sequences and perform the task blindfolded sitting at 90 cm  
203 distance from the speakers.

#### 204 **2.1.4 EEG acquisition**

205 The EEG was recorded with a Biosemi Active Two system  
206 (<https://www.biosemi.com/products.htm>) with 128 Ag-AgCl active electrodes at a sampling rate of 512 Hz.  
207 Recording sites included standard 10-20 system locations as well as intermediate positions (position  
208 coordinates can be found at: <https://www.biosemi.com/headcap.htm>). The magnitude of electrode offset,  
209 referenced to the common mode sense (CMS), was held below  $\pm 50$  mV.

#### 210 **2.1.5 Analysis**

211 Data analysis was performed using the Letswave5 toolbox  
212 (<https://github.com/NOCIONS/Letswave5>) and the FieldTrip toolbox (Oostenveld et al., 2011) running on  
213 Matlab\_R2016b (MathWorks, USA), custom-build scripts in Matlab\_R2016b and RStudio.

#### 214 **2.1.6 Pre-processing**

215 A fourth order Butterworth band-pass filter with cut-off values of 0.1-100 Hz was applied to the

216 raw continuous EEG data of each participant. Electrical noise at 50 Hz, 100 Hz and 150 Hz was attenuated  
217 with a FFT multi-notch filter with a width of 0.5 Hz. Data were then downsampled to 256 Hz to facilitate  
218 data handling and storage. Subsequently, data were segmented into 69 s long epochs (we will use the term  
219 epoch in the analysis sections to refer to the EEG data relative to one sequence of stimulation) to include 2  
220 s before the onset of the fade-in and 3 s after the offset of the fade-out of the stimulation sequences. At  
221 this stage, after visual inspection of the data, four subjects were excluded from further analysis as their EEG  
222 trace was highly contaminated by artefacts. In the remaining sixteen participants, noisy channels were  
223 linearly interpolated with the closest neighboring channels (three/four, considering electrodes representing  
224 the full area around the interpolated one). This procedure was carried on six participants with no more  
225 than 5% of the electrodes (Bottari et al., 2020; Retter et al., 2020) being interpolated in each participant  
226 (mean number of channels interpolated considering all sixteen participants is 1, range: 0-6; of the channels  
227 interpolated across the six participants, 6 were posterior-occipital electrodes, 2 central parietal, 1 central, 1  
228 temporal, 1 fronto-temporal, 4 fronto-central and 1 anterior-frontal). The same analyses performed on the  
229 ten participants on which no channel interpolation was performed and on the entire group (with  
230 interpolation) led to very similar results. Epochs that presented multiple artefacts after channel  
231 interpolation were removed, with no more than one epoch per condition per participant being excluded.  
232 All one hundred twenty-eight EEG channels were then re-referenced to the common average of all  
233 electrodes.

#### 234 **2.1.7 Frequency domain analysis**

235 Considering the frequency resolution ( $1 / \text{duration of the sequence}$ ) and the frequency of  
236 stimulation (target frequency), pre-processed data were re-segmented so as to contain an integer of voice  
237 presentation cycles to avoid overspill of the target-rate response in the frequency domain. Therefore,  
238 epochs were re-segmented excluding fade-in and -out and had a final length of 60 s. For each condition  
239 and participant separately, epochs were averaged in the time domain to attenuate EEG activity not in  
240 phase with the auditory stimulation. A fast Fourier transformation was applied, resulting in amplitude  
241 spectra for each channel, condition and subject. Amplitude spectra ranged from 0 to 128 Hz and had a very  
242 high resolution of 0.0167 Hz (i.e.,  $1/60\text{s}$ ), thus allowing to isolate responses at the frequencies of interest

243 and their harmonics. Then, we determined the number of significant harmonics at the group level for  
244 target and base frequencies: for each condition separately, we computed the grand average across  
245 subjects, pooled all channels together and calculated z-scores on these averaged spectra including as  
246 baseline 20 surrounding frequency bins (10 bins on each side excluding the immediately adjacent bins, the  
247 local minimum and the local maximum; e.g. Retter & Rossion, 2016). Harmonics of the target and base  
248 frequencies were considered as significant if their relative z-scores were higher than 2.32 (i.e.  $p < 0.01$ , 1-  
249 tailed, signal > noise). Consecutive significant harmonics were considered, excluding frequencies  
250 corresponding to the base-rate responses for the count of target-rate significant harmonics. Responses are  
251 represented as topographical head maps summing baseline subtracted amplitude spectra at significant  
252 harmonics for target and base frequencies separately, where baseline was calculated as for the calculation  
253 of z-scores. Baseline subtraction prior to quantification of the response enables to take into account the  
254 fact that different frequency bands are differentially affected by noise in EEG recordings (Luck, 2014), with  
255 typically higher noise at low frequencies (below 1 Hz) and in the alpha frequency band (8-13 Hz). We also  
256 compared the sum of the baseline subtracted amplitude of the significant harmonics as elicited by the  
257 standard and the scrambled sequences (standard > scrambled, Bonferroni correction for the 128  
258 electrodes). To compute this comparison, we considered the highest number of significant harmonics in  
259 any of the two conditions (here, *standard*) knowing that including baseline-subtracted activity at non-  
260 significant harmonics to compute the overall response is not detrimental (i.e., adding zeroes). The  
261 electrodes that were significant for the standard > scrambled comparison were considered to define the  
262 voice-selective region-of-interest (ROIvoice).

263 To assess the robustness of the method to identify voice-selective responses with an even shorter  
264 acquisition time, we conducted the same analysis to individuate significant harmonics considering only the  
265 responses elicited by the first stimulation sequence for each condition (i.e., one minute of recording).

266 Lastly, we performed source localization to identify the generators of the voice-selective response.  
267 Source localization was implemented here with Dynamic Imaging of Coherent Sources (DICS, Gross et al.,  
268 2001) following the method as described in Popov et al., 2018. Using the cross-spectral density (CSD)  
269 calculated at the sensor level, DICS estimates the interaction between sources at a particular frequency: in

270 this case, at the voice presentation frequency (1.333 Hz). This beamformer was chosen since it yields lower  
271 localization error despite low SNR when compared to other current density measures (Halder et al., 2019).  
272 To attenuate brain activity not in phase with the auditory stimulation, all epochs were averaged in the time  
273 domain, then across all subjects for standard and scrambled sequences separately; consequently, a Fourier  
274 transform was applied to compute the CSD. The forward model was computed with the segmentation of  
275 the MRI152 template, based on which a headmodel was generated using the boundary element model  
276 (BEM), characterizing the current conduction and propagation properties in surfaces of scalp, skull and  
277 brain. Sources were placed in the brain part of the volume conduction headmodel with a resolution of 5  
278 mm. Further, we performed a manual co-registration of the headmodel and Biosemi electrode coordinates  
279 using rotation, translation and scaling of the electrodes on the scalp to match our best visual estimate. Due  
280 to the imprecise co-registration of the forward model, as we did not have individual participants' MRI and  
281 precise electrode location on the scalp, we did not focus on the exact anatomical areas of the brain  
282 generators, but limited our attention to compare the voxel-by-voxel activity (i.e. coherence) between the  
283 two conditions. A common spatial filter was computed by appending the data of the two conditions to  
284 localize each condition. A regularization parameter of 5% was used. Then, we calculated the difference of  
285 coherence values between the standard and scrambled conditions taking the whole brain into  
286 consideration to estimate an overall activity at the target frequency. We hypothesized to obtain higher  
287 coherence values for the standard condition.

288         Although source analysis is introduced to suggest a link with previous neuroimaging studies, results  
289 should be interpreted cautiously, not only because of the indeterminate nature of source localization from  
290 scalp voltage potentials but also because we did not collect MRI scans of individual participants, nor the  
291 electrode positions on their scalp during the EEG sessions, important elements that would enhance the  
292 precision and accuracy of source localization (Akalin Acar and Makeig, 2013). We therefore consider the  
293 results of the source localization for visualization purpose only and the main statistical inferences were  
294 done on the scalp data.

## 295         **2.2 Experiment 2 – Voice versus musical instruments controlled for low level acoustic properties**

296         Materials and methods were the same as for experiment 1 unless specified below.

297 **2.2.1 Stimuli**

298 Sounds were extracted from a database provided by Agus and collaborators (Agus et al., 2017;  
299 Goto et al., 2003). Stimuli were 128 ms, therefore the base and target frequencies of what we will refer to  
300 as *harmonic sequences* were approximately 7.813 Hz and 2.604 Hz, respectively. Vocal stimuli (16  
301 exemplars) consisted in vowels /a/, /e/, /i/ and /o/ sung in the note A3 by two male and two female  
302 singers. Non-vocal sounds consisted in sixteen different musical instruments playing the note A3 (oboe,  
303 clarinet, bassoon, saxophone, trumpet, trombone, horn, guitar, mandolin, ukulele, harpsichord, piano,  
304 marimba, violin, viola, and cello, for a total of 16 stimuli). Importantly, vocal and non-vocal sounds  
305 implemented for this sequence type were matched for pitch ( $M = 223.5$  Hz,  $SD = 7.1$ Hz for voices,  $M =$   
306  $220.6$  Hz,  $SD = 1.85$  Hz for instruments, Welch Two Sample t-test  $t(17.03) = 1.56$ ,  $p = 0.14$ ), spectral center  
307 of gravity (Mann-Whitney Test,  $W = 107$ ,  $p = 0.45$ ) and harmonicity to noise ratio ( $M = 20.9$  dB,  $SD = 2.5$  dB  
308 for voices,  $M = 18.9$  dB,  $SD = 5.0$  dB for instruments, Welch Two Sample t-test  $t(21.8) = 1.45$ ,  $p = 0.16$ ,  
309 Figure 1E). Stimuli were equalized in overall energy (RMS) and their RMS value was set as to match the  
310 energy of the sounds of experiment 1. Sounds were then faded-in and -out with 10 ms ramps in order to  
311 facilitate individual sounds segregation and avoid clicking.

312 **2.2.2 Procedure**

313 *Harmonic sequences* were generated following the same procedure as reported for experiment 1,  
314 presenting sounds one after another with each third sound being a voice. Sequences were 65,5 s long  
315 including 2 s of fade-in and -out. As in experiment 1, individual sequences were created before testing for  
316 each repetition and for each individual participant and included six attentional targets consisting in sounds  
317 played at a lower volume. Participants were required to listen to four different harmonic sequences and  
318 press a button whenever they perceived a sound played in a lower volume sitting blindfolded at 90 cm  
319 from the speakers.

320 **2.2.3 Analysis**

321 Data were analyzed as in experiment 1 with the epochs being re-segmented from 2.048 s after the  
322 onset of the sequences (to exclude fade-in and to start segmenting from the onset of the first sound at  
323 100% volume) and had a final length of 59.9 s to contain an integer of voice presentation cycles and avoid

324 overspill of the target-rate response in the frequency domain. The number of significant harmonics for the  
325 responses at the target and base frequencies were calculated as in the previous experiment considering all  
326 four stimulation sequences or the first sequence alone. We then performed a region-of-interest analysis by  
327 averaging the sum of the baseline subtracted amplitude of the significant harmonics of the target of the  
328 electrodes of the ROIvoice as defined in experiment 1 and contrasted the resulting activity against 0.

### 329 **2.3 Experiment 3 - Behavioral detection of voices**

330 To validate that the sounds presented in the two EEG experiments could effectively be categorized  
331 as vocal/non-vocal sounds and to assess the effectiveness of the sound scrambling procedure in altering  
332 intelligibility, we conducted a behavioral experiment in which participants had to classify all sounds,  
333 presented either in short sequences or in isolation, as vocal or non-vocal sounds.

#### 334 **2.3.1 Participants**

335 Sixteen participants (age range 18-26 years, 9 female), four of which had previously participated in  
336 the EEG experiments, took part in the behavioral experiment. All participants reported normal or corrected  
337 to normal vision, normal hearing and no history of psychiatric or neurological disorders. The experiment  
338 was approved by the local ethical committee of the University of Louvain (Project 2016-25); all participants  
339 provided written informed consent and received financial compensation for their participation.

#### 340 **2.3.2 Stimuli**

341 Auditory stimuli were the same as for experiments 1 and 2, all equalized so to have the same  
342 overall energy (RMS) and faded-in and -out with 10 ms ramps.

#### 343 **2.3.3 Procedure**

344 Participants listened to sounds corresponding to the three sequence types of experiments 1 and 2  
345 (*standard*, *scrambled* and *harmonic*) that were presented either embedded in short sequences of five  
346 sounds (task *sequence*) or in isolation (task *isolation*). For the *sequence* task, short sequences were created  
347 so that they could contain either one vocal sound or none (50% / 50% of occurrences). In particular, when a  
348 vocal sound was presented in a short sequence, it was inserted as the third sound to mimic the structure of  
349 sequences implemented for the electroencephalographic experiments. For each condition, 80 sequences  
350 were created (40 with one voice, 40 without voices), for a total of 240 trials (1 short sequence of the

351 behavioral experiment = 1 trial). In the *isolation* task, for the sequence types *standard* and *scrambled* we  
352 presented 33 vocal and 67 non-vocal sounds extracted randomly for each participant to reproduce the 1 to  
353 2 ratio of vocal and non-vocal stimuli presented in sequences in the EEG experiment. For the *harmonic*  
354 sequence, we presented all 16 vocal and 16 non-vocal stimuli. Sounds from each of the three conditions  
355 were presented once in a randomized order, for a total of 132 trials (1 sound = 1 trial). The *sequence* and  
356 *isolation* tasks were presented one after another. Each trial consisted in the presentation of one short  
357 sequence (*sequence*)/one sound (*isolation*) after which participants had to indicate whether they heard a  
358 voice or not with a button press and a response was required in order to initiate the following trial.  
359 Participants performed the task blindfolded. The experiment was implemented on Matlab\_R2016b  
360 (MathWorks, USA) using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli,  
361 1997).

### 362 **3. Results**

#### 363 **3.1 Experiment 1 – Voice versus object sounds**

364 We expected clear responses at the base frequency (BF, 4 Hz) and harmonics (multiples of BF: 2BF,  
365 3BF, etc.) for both the standard and the scrambled sequences, a response at the base frequency reflecting  
366 shared processes between all sounds. Then, we predicted to observe – or not, depending on the sequence  
367 type – responses at the target frequency (TF, 1.333Hz) and the harmonics. Critically, a response at the  
368 target frequency would arise only if the participant’s brain successfully discriminates human voices from  
369 other sounds and generalizes across voices. We predicted that the standard sequences would elicit a voice-  
370 selective response reflecting selective responses to vocal versus non-vocal sounds. We also hypothesized  
371 that if voice-selective responses evoked by the standard condition were the mere by-product of frequency  
372 content, the scrambled condition would have elicited responses quantitatively (in terms of magnitude of  
373 the response) and qualitatively (in terms of topographical distribution of the response) similar to the  
374 standard condition.

375

##### 376 **3.1.1 Base frequency**

377 We observed significant responses for the first two harmonics of the base stimulation frequency,  
378 i.e. at 4 and 8 Hz, for both the standard and scrambled sequences. The scalp topographies of the two  
379 conditions obtained summing baseline corrected amplitudes at the two significant harmonics did not differ,  
380 suggesting that individual sounds were similarly processed between the standard and scrambled  
381 conditions, with responses peaking over central and occipital electrodes (Figure 2).

### 382 **3.1.2 Target frequency**

383 The standard sequence elicited robust voice-selective responses that were significant at the group  
384 level for the first four harmonics of the target frequency (at 1.333 Hz, 2.666 Hz, 5.333 Hz and 6.666 Hz). For  
385 the scrambled sequence, we observed a weak but significant response only at the first harmonic of the  
386 target frequency (at 1.333 Hz). We quantified voice-selective responses as the sum of the baseline  
387 subtracted amplitudes of the highest number of significant harmonics in any of the two conditions (here:  
388 standard, four harmonics) knowing that including baseline-subtracted activity at non-significant harmonics  
389 to compute the overall response is not detrimental (i.e., adding zeroes; Retter et al., 2018). For the  
390 standard condition, voice-selective responses peaked bilaterally at superior temporal electrodes (Figure 2):  
391 TP8h, CP6, T8h, T8 on the right hemisphere and T7h, T7, TP7 on the left hemisphere (contrasting the  
392 response against zero, one-sided t-test, reported p-values are Bonferroni corrected, Cohen's d values are  
393 reported referred to as "d", TP8h:  $t(15) = 6.68$ ,  $p = 0.0005$ ,  $d = 1.67$ ; CP6:  $t(15) = 5.51$ ,  $p = 0.0038$ ,  $d = 1.38$ ;  
394 T8h:  $t(15) = 6.89$ ,  $p = 0.0003$ ,  $d = 1.72$ ; T8:  $t(15) = 7.16$ ,  $p = 0.0002$ ,  $d = 1.79$ ; T7h:  $t(15) = 5.62$ ,  $p = 0.0031$ ,  $d$   
395  $= 1.40$ ; T7:  $t(15) = 5.44$ ,  $p = 0.0043$ ,  $d = 1.36$ ; TP7:  $t(15) = 5.56$ ,  $p = 0.0035$ ,  $d = 1.39$ ), the topography of the  
396 response being consistent across participants (Figure 3). No electrode reached significance when we  
397 computed the same contrast for the scrambled condition. Overall, in regions where the response was  
398 peaking for the standard condition, the amplitude of the response to voice-scrambled stimuli was of 50.6%  
399 of the response to voices for the left ROI (T7h, T7, TP7) and only 18.8% for the right ROI (TP8h, CP6, T8h,  
400 T8; Figure 2F). Moreover, the magnitude of the responses to the standard and scrambled conditions over  
401 these two region-of-interests did not correlate across participants (Spearman's rho correlation, left ROI:  $r_s =$   
402  $0.11$ ,  $p = 0.68$ , right ROI:  $r_s = 0.14$ ,  $p = 0.62$ ; Figure 2G). This suggests that, although scrambled voices could  
403 elicit a response, frequency content alone was not enough to elicit a voice-selective response as recorded

404 with the standard sequence. We further investigated that by comparing the responses elicited at the target  
405 frequency by the standard and the scrambled sequences; although one of the advantages of the FPAS  
406 paradigm is that it does not require a direct comparison between conditions, we decided to include this  
407 extra step as a proof of principle since we introduce oddball fast periodic stimulation with high-level,  
408 naturalistic sounds for the first time here. First, for each condition, participant and electrode separately we  
409 summed the responses of the highest number (i.e., four) of significant harmonics in any of the two  
410 conditions. Then, comparing the responses for each participant and electrode (standard > scrambled,  
411 paired-sample t-test, Bonferroni corrected), we isolated four significant superior temporal electrodes over  
412 the right hemisphere: TP8h, CP6, C6 and T8 (TP8h:  $t(15) = 6.21$ ,  $p = 0.0011$ ,  $d = 1.55$ ; CP6 :  $t(15) = 5.02$ ,  $p =$   
413  $0.0097$ ,  $d = 1.26$ ; C6:  $t(15) = 4.71$ ,  $p = 0.0179$ ,  $d = 1.18$ ; T8:  $t(15) = 4.60$ ,  $p = 0.0223$ ,  $d = 1.15$ , Bonferroni  
414 corrected). Non-parametric testing (Winkler et al., 2014) of the standard > scrambled comparison led to  
415 very similar results and the choice of a one-sided comparison was made with the a priori assumption that  
416 the scrambled condition would have elicited a target response as high - if voice responses could have been  
417 explained by frequency content alone - or smaller than the one elicited by the standard sequence. Finally, a  
418 region-of-interest was defined considering the four electrodes identified as above (ROIvoice; Figure 2).

419 To assess whether FPAS was a suitable tool to investigate voice-selectivity at the individual level,  
420 we calculated whether these responses were significant in every subject (Liu-Shuang et al., 2016). For each  
421 participant, we considered the amplitude spectrum and we pooled together all channels. We chunked  
422 epochs that were centered around the harmonics of the target frequency that were significant at the group  
423 level (1.333 Hz, 2.666 Hz, 5.333 Hz and 6.666 Hz) and that contained 11 frequency bins on each side. We  
424 then summed these epochs together and computed the z-scores at the target frequency considering as  
425 baseline the 20 surrounding frequency bins (10 on each side, excluding the immediately adjacent bin).  
426 Considering as significant responses whose relative z-scores was higher than 1.64 (i.e.  $p < 0.05$ , 1-tailed,  
427 signal > noise), we were able to find significant voice-selective responses in 13 out of 16 participants (with  
428 only 4 minutes of recordings).

429 To assess the robustness of the method with an even shorter acquisition time, we then performed  
430 the same analytical steps done to calculate the number of significant harmonics at the group level

431 considering the first sequence of recording only. For the standard sequence, we were able to identify voice-  
432 selective responses that were significant at the group level even with one minute of recording only (1  
433 significant harmonic: 1.333 Hz). The signal-to-noise ratio (SNR) of the response at right superior temporal  
434 electrodes (ROIvoice) as a function of number of stimulation sequences (i.e., minutes of recordings, as each  
435 sequence is one minute long) is presented for visualization purposes in Figure 2C.

436 A stronger voice-selective response in the standard condition was observed when compared to the  
437 scrambled condition at the source level as well. After implementing source localization, the final voxel  
438 coherence values were compared for the two conditions (standard > scrambled) and interpolated to the  
439 MRI152 template. Then, the voxels with intensity above the 95<sup>th</sup> percentile were selected, as illustrated in  
440 figure 2B. The maximum value obtained of 0.32 (min-max range: [0 1]) indicates voxel preference for voice  
441 presentation frequency (i.e. 1.333 Hz) for the standard over the scrambled sequence. Despite the imprecise  
442 source localization due to the limitations outlined in the method section (lack of individual coregistration  
443 between electrodes position and brain anatomy), the position of the source reconstructed effect of interest  
444 (Figure 2B) lies in the vicinity of the known location of TVAs (Belin et al., 2002, 2000) and are in line with  
445 results showing that right anterior STS regions respond more strongly to non-speech vocal sounds than  
446 their scrambled versions (Belin et al., 2002).

### 447 **3.2 Experiment 2 – Voice versus musical instruments controlled for low level acoustic properties**

448 We expected to observe a response at the base presentation frequency (7.813 Hz) and its  
449 harmonics, this response reflecting processes that are shared among vocal and non-vocal sounds. More  
450 crucially, we predicted that, if voice-selectivity is not solely driven by harmonicity and/or pitch of the  
451 sounds, we would observe a target-rate response to the harmonic sequences as in these sequences vocal  
452 and non-vocal sounds did not differ for these low-level acoustic features.

453

#### 454 **3.2.1 Base frequency**

455 There was a significant base-rate response for the first two harmonics: at 7.813 Hz and 15.625 Hz,  
456 with responses peaking over central and occipital electrodes (Figure 4). The topography of the response  
457 was qualitatively similar to the base-rate responses obtained in experiment 1.

458 **3.2.2 Target frequency**

459 We observed a significant voice-selective response for the first two harmonics (2.604 Hz and 5.208  
460 Hz). Voice-selective responses peaked over central and superior temporal electrodes bilaterally, the scalp  
461 distribution of the response being highly similar to the voice-selective response found in the standard  
462 sequence (Figure 4) and being reliable across participants. We then performed a region-of-interest analysis  
463 considering the right superior temporal electrodes (ROIvoice) as defined in experiment 1. Baseline  
464 subtracted amplitudes at the two significant harmonics were summed for each electrode individually and  
465 the resulting responses at the electrodes of the ROIvoice were then averaged together for every  
466 participant. One data point was excluded as it deviated more than three standard deviations from the  
467 mean of the group and responses were significant against zero ( $M = 0.152 \mu\text{V}$ ,  $SD = 0.087 \mu\text{V}$ ,  $t(14) = 6.78$ ,  $p$   
468  $= 4.436 \times 10^{-6}$ ,  $d = 1.75$ , 1-tailed t-test).

469 Voice-selective responses were already present after one minute of recording, showing the  
470 resilience of FPAS even with very short acquisition time (one harmonic significant, the second: 5.208 Hz,  
471 with two minutes of recording the first two harmonics reached significance at the group level; Figure 4).

472 As for the standard condition, we then assessed significance of voice-selective responses at the  
473 individual level with the same procedure. 15 out of 16 participants showed a significant response (z-score  
474 higher than 1.64, i.e.  $p < 0.05$ , 1-tailed, signal > noise).

475

476 **3.3 Experiment 3 - Behavioral detection of voices**

477 Responses to the *sequence* and *isolation* tasks were analyzed according to signal detection theory.  
478 Specifically, sensitivity indices related to the participants' ability to detect a voice when present was  
479 assessed using d-prime (Figure 5). D-prime ( $d'$ ) constitutes an unbiased quantification of performance in  
480 detection tasks as it takes into account both hits and false alarms (Macmillan and Creelman, 2004; Tanner  
481 and Swets, 1954). Data points were considered as outliers when deviating from the mean of the group of  
482 more (or less) than three times the standard deviation of the group in at least one condition/task, leading  
483 to the exclusion of one participant. We first checked whether performance was above chance ( $d' = 0$ ) for  
484 each condition and for the *sequence* and the *isolation* task separately. Participants performed above

485 chance for all conditions in the sequence (t-test, 1-tail, standard:  $d'$  values mean  $M = 4.11$ ,  $SD = 0.45$ ,  $t(14)$   
486  $= 35.30$ ,  $p = 2.2 \times 10^{-15}$ , Cohen's  $d = 9.11$ ; scrambled:  $M = 0.29$ ,  $SD = 0.30$ ,  $t(14) = 3.75$ ,  $p = 0.001$ ,  $d = 0.97$ ;  
487 harmonic:  $M = 1.91$ ,  $SD = 0.77$ ,  $t(14) = 9.58$ ,  $p = 7.8 \times 10^{-8}$ ,  $d = 2.47$ ) and in the isolation task (t-test, 1-tail,  
488 standard:  $M = 4.25$ ,  $SD = 0.46$ ,  $t(14) = 35.71$ ,  $p = 1.8 \times 10^{-15}$ ,  $d = 9.21$ ; scrambled:  $M = 0.16$ ,  $SD = 0.21$ ,  $t(14) =$   
489  $2.97$ ,  $p = 0.005$ ,  $d = 0.77$ ; harmonic:  $M = 3.30$ ,  $SD = 1.24$ ,  $t(14) = 10.29$ ,  $p = 3.3 \times 10^{-8}$ ,  $d = 2.66$ ). Statistical  
490 comparisons of conditions were then performed separately for the two tasks using repeated measures  
491 ANOVAs. Whenever Mauchly's test indicated that the assumption of sphericity had been violated, we  
492 applied a Greenhouse-Geisser correction to the degrees of freedom. For the *sequence* task, we found a  
493 significant effect of condition ( $F(2,28) = 207.39$ ,  $p = 1.6 \times 10^{-17}$ ,  $\eta^2 = 0.898$ ) and post-hoc pairwise  
494 comparisons showed that all conditions differed one from another (standard vs. scrambled,  $p < 2 \times 10^{-16}$ ;  
495 standard vs. harmonic,  $p = 7.1 \times 10^{-9}$ ; scrambled vs. harmonic,  $p = 1.5 \times 10^{-6}$ ; Bonferroni corrected). The  
496 same pattern of performance was found when sounds were presented in isolation ( $F(1.20, 16.86) = 134.23$ ,  
497  $p = 6.8 \times 10^{-10}$ ,  $\eta^2 = 0.845$ ; pairwise comparisons: standard vs. scrambled,  $p < 2 \times 10^{-16}$ ; standard vs.  
498 harmonic,  $p = 0.038$ ; scrambled vs. harmonic,  $p = 2.7 \times 10^{-7}$ ; Bonferroni corrected). Although performance  
499 was above chance for the scrambled sounds,  $d$ -prime scores were significantly lower than the one achieved  
500 in the standard condition (Figure 5), suggesting that our frequency scrambling effectively disrupted the  
501 intelligibility of the sounds.

#### 502 4. Discussion

503 Similarly to the issue of category-selectivity in human visual cortex (Bracci et al., 2017; Peelen and  
504 Downing, 2017; Rice et al., 2014), studies have attempted to determine whether category-selectivity in  
505 auditory cortices is mostly driven by a biased tuning toward low-level acoustic features or if categorization  
506 responses go beyond the acoustic properties of sound and therefore represent a more abstract  
507 representation of voices (Giordano et al., 2013; Leaver and Rauschecker, 2010). In fact, as sounds tend to  
508 be acoustically similar within an auditory category and dissimilar between categories, differences in cortical  
509 responses could be a mere reflection of different acoustic properties across categories of sounds (Ogg et  
510 al., 2019; Staeren et al., 2009). One approach to address this question is to test for low-level featural  
511 coding. However, although studies using artificial stimuli allow for a careful control of low-level acoustic

512 properties (Lewis et al., 2009; Patterson et al., 2002; Warren et al., 2005), they usually lack ecological  
513 validity and underestimate the issue of stimulus-driven response correlation (Norman-Haignere and  
514 McDermott, 2018). Moreover, artificial stimuli may fail in eliciting brain activation in a (behaviorally)  
515 relevant way, as evidenced by a study revealing different tonotopic maps obtained with natural sounds and  
516 pure tones (Moerel et al., 2012).

517 In this study, we developed a Fast Periodic Auditory Stimulation (FPAS) paradigm as a powerful mean to  
518 investigate voice-selectivity in the brain with the aim of disentangling between a categorization response to  
519 voices and the contribution of low-level acoustic features that are typical of voices (e.g. high harmonicity,  
520 characteristic frequency ranges, specific change of energy over time) with EEG. The frequency constraint of  
521 this approach allowed us to individuate robust voice-selective responses objectively – at known stimulation  
522 frequencies – and automatically: not only participants did not have to overtly respond to voices, thus  
523 avoiding the contamination of the response from attentional and decisional processes (Levy et al., 2003;  
524 Von Kriegstein et al., 2003), but also no subtraction between responses elicited by different auditory  
525 categories was required. That is, while traditional M/EEG approaches investigate whether there are  
526 differences in isolated responses elicited by different classes of stimuli (Charest et al., 2009; De Lucia et al.,  
527 2010; Levy et al., 2003; Murray et al., 2006), in our paradigm this differentiation is implicit. Moreover, the  
528 relatively low-speed presentation of stimuli required by many traditional experimental paradigms preclude  
529 from the possibility of presenting a high number of stimuli that could be representative enough of an  
530 auditory category and therefore responses observed to such a subset of voice samples might not reflect a  
531 *generalized* response to voices (Giordano et al. 2013). In addition, low-speed presentation of stimuli might  
532 fail in fully characterising voice processes as they occur in daily-life, since we are experts in extracting voice  
533 features almost effortlessly in highly dynamic acoustically changing environments.

534 For a voice-specific response to be captured with the FPAS paradigm, two processes need to occur:  
535 the brain has to concurrently *discriminate* voices from non-vocal sounds and to *generalize* this selective  
536 response across diverse vocal samples for a response at the target (i.e. voice presentation) rate to occur.  
537 FPAS therefore not only allows to characterize a general voice-selective response, as it is elicited by  
538 heterogeneous vocal samples and not from a specific subset of those, but also not to cancel out processes

539 elicited by voices that are shared by other sound categories. This can be accomplished in a very short  
540 acquisition time (i.e. four minutes or even less) and with a high SNR (Figure 2C, e.g., up to 7, or 600% of  
541 amplitude increase with 4 stimulation sequences).

542 To isolate voice-selective responses that could not be merely explained by low-level acoustic  
543 features, we implemented two EEG experiments using the FPAS principle. In the first experiment,  
544 participants were presented with two different types of FPAS sequences. In the standard sequence, vocal  
545 and non-vocal samples were selected to be as heterogeneous as possible to represent the high variability of  
546 sounds of a given category (e.g., voices from speakers from different ages, sex, emotional state with speech  
547 and non-speech vocalizations) as encountered in natural environment, as well as to minimize the potential  
548 contributions of low-level acoustic features in the voice-selective response (controlling by variability).  
549 Specifically, low level acoustic properties would have to vary periodically to participate in the target-specific  
550 responses, and the high variability of the voice samples adopted should prevent that. These sounds were  
551 then scrambled using small frequency bins (after FFT) in order to generate a sequence in which scrambled  
552 sounds had similar frequency content as the original stimuli (Figure 1C) but were not recognizable anymore  
553 (Figure 5). We measured robust voice-selective responses at superior temporal electrodes that were  
554 significant in the vast majority of the participants with only 4 minutes of recording (Figure 2). Moreover,  
555 these responses remained significant at the group level when restricting the analysis to the first minute of  
556 recording only, highlighting the robustness of the method even with an extremely short acquisition time.  
557 Voice-selective responses could not have been explained by frequency content alone: although one of the  
558 advantages of FPAS is that it does not require an explicit comparison across conditions, here, as an extra  
559 proof of principle, we compared the responses elicited by the standard and scrambled sequences,  
560 highlighting a response expressing over right superior temporal electrodes. This preference also emerged at  
561 the source space: although source localization as implemented in our study presents limitations that could  
562 hinder the accuracy of our results (see methods section), we localized a standard > scrambled preference  
563 over the right superior temporal gyrus and sulci. The observed regions lie in the proximity of the TVAs and  
564 are in line with results showing that the right anterior STS regions respond more strongly to non-speech  
565 vocal sounds than their scrambled versions (Belin et al., 2002).

566 It has to be noted that the scrambled condition elicited a weak but yet significant response at the  
567 (scrambled) voice presentation rates: we think there might be two - not mutually exclusive - explanations  
568 for this weak response. First, this response might be due to the low-level acoustic features shared by voices  
569 and scrambled voices (i.e. frequency content): preferential response biases towards acoustic features  
570 peculiar of voices have been observed in voice-selective regions (Moerel et al., 2012) and, despite the fact  
571 that voice-selective responses elicited by the standard condition could not be well explained by low-level  
572 acoustic features alone, these features may nevertheless weakly contribute to the response. Second,  
573 although the scrambling procedure disrupted the intelligibility of the sounds, with original sounds being  
574 more accurately recognized as voices or not than scrambled sounds, participants' performance in  
575 categorizing scrambled sounds was above chance level, suggesting that some residual sound recognizability  
576 might have still been present.

577 To further investigate the nature of voice-selective responses, we designed a second FPAS  
578 experiment using sequences built from sung vowels and musical instruments that were matched in terms  
579 of pitch, spectral center of gravity and harmonicity to noise ratio. The observation of robust voice-selective  
580 responses despite controlling for the above-mentioned acoustic features speaks in favor of a categorization  
581 response to voices that is at least partially independent from some of the most intrinsic acoustic features of  
582 voices. The similar scalp topographies elicited by the standard and harmonic sequences suggest a similarity  
583 between the selective responses to voices elicited in the two conditions. However, the voice-selective  
584 response in the standard sequences was larger in amplitude as compared to the response of the harmonic  
585 sequence. Different factors might account for this difference. First, the higher amplitude of response  
586 observed in the standard sequence could be due to voices being more easily discriminated from non-vocal  
587 sounds, as pointed out by the behavioral data. In fact, even if an overt response to voices is not necessary  
588 to elicit a target rate specific response, the easiness at which a voice is perceived could have impacted the  
589 amplitude of brain responses. Second, while vocal stimuli of the harmonic sequence were accurately  
590 chosen to be matched in acoustic properties with the sounds of musical instruments, it could be argued  
591 that those vocal stimuli represent a subset of voices, and thus that the strongest response in the standard  
592 condition reflects the response to a more heterogeneous and representative sample of voices of that

593 condition. The choice of the frequencies of stimulation could also have impacted on the magnitude of the  
594 responses (Ding et al., 2006; Regan, 1966; Retter et al., 2020): while all parameters proved effective in  
595 eliciting target-rate responses, further studies would be needed to indicate which parameters are optimal  
596 to capture voice-selective responses, as addressed in the case of the implementation of the frequency  
597 tagging approach in high-level vision (e.g., Retter et al., 2020; Alonso-Prieto et al., 2013). Finally, systematic  
598 differences in low-level acoustic features between vocal and non-vocal sound potentially present in the  
599 standard sequence could have boosted the categorization response to voices. In fact, feature dependence  
600 is not in conflict with a categorical coding hypothesis (Bracci et al., 2017), and preferential response biases  
601 observed in voice regions to specific acoustic features such as low frequencies (Moerel et al., 2012),  
602 harmonic structure (Lewis et al., 2009) and spectrotemporal modulations (Santoro et al., 2017), could serve  
603 as a scaffold or facilitate a higher level categorical responses to voices.

604 In summary, we objectively defined human voice-selective responses independent from low-level  
605 acoustic cues that are characteristic of voices with high SNR and in a very short acquisition time using an  
606 original Fast Periodic Auditory Stimulation (FPAS) approach. Although it is possible that other acoustic  
607 features that were not explicitly controlled for might be at the origin of the recorded responses, the nature  
608 of the FPAS design makes it unlikely, as said features should be systematically present in all voices and  
609 absent in non-vocal sounds. In other words, activity in voice-selective regions could not be only, or even  
610 substantially, accounted for by any basic acoustic parameter tested.

611 While the goal of the current study was to investigate the existence of a voice-selective response  
612 partially independent from some acoustic features, the FPAS paradigm we developed could be a valuable  
613 tool for the study of auditory perceptual categorization in the human brain, extending to other categories.  
614 Moreover, the high SNR of this technique achievable in a very short acquisition time (i.e., significant  
615 responses were observed with one minute of recording) and the fact that no overt response to specific  
616 stimuli is required, makes this approach highly promising for studying voice perception in children and  
617 clinical populations. Our findings therefore advance our understanding of voice-selectivity in the brain and  
618 our method provides an essential foundation for understanding its development in typical and atypical  
619 populations.

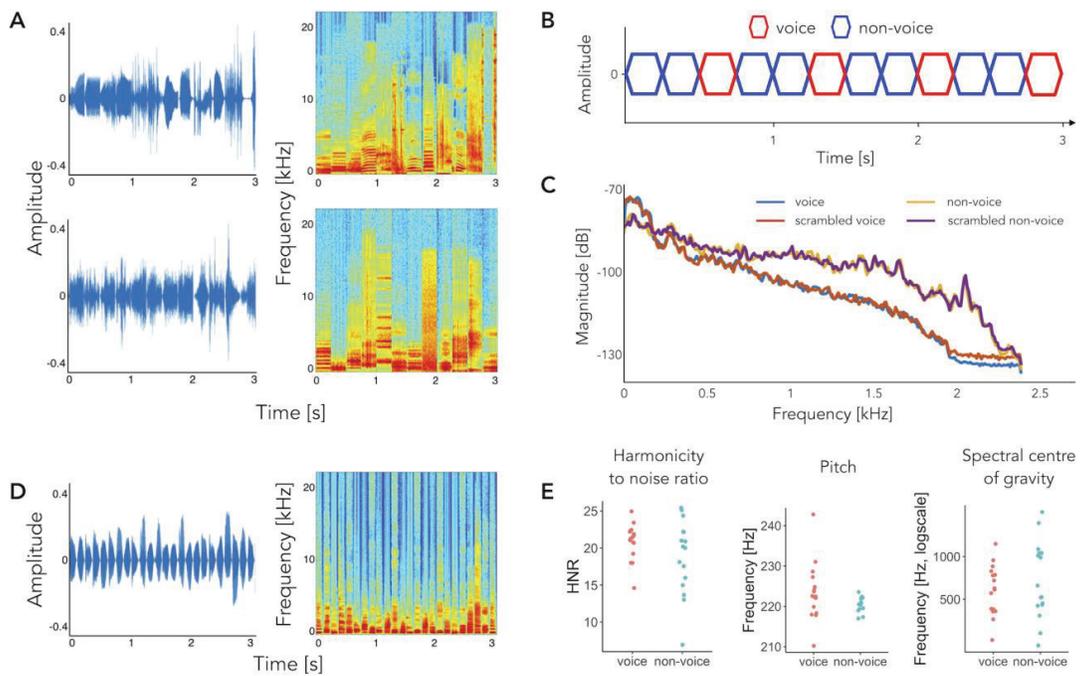
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- 725



726

727 **Figure 1. Experimental design for experiments 1 (A, B ,C) and 2 (D, E).** A) 3 s excerpts of the sequences for

728 the standard (top) and scrambled (bottom) sequences (left) with their relative spectrograms (right). B)

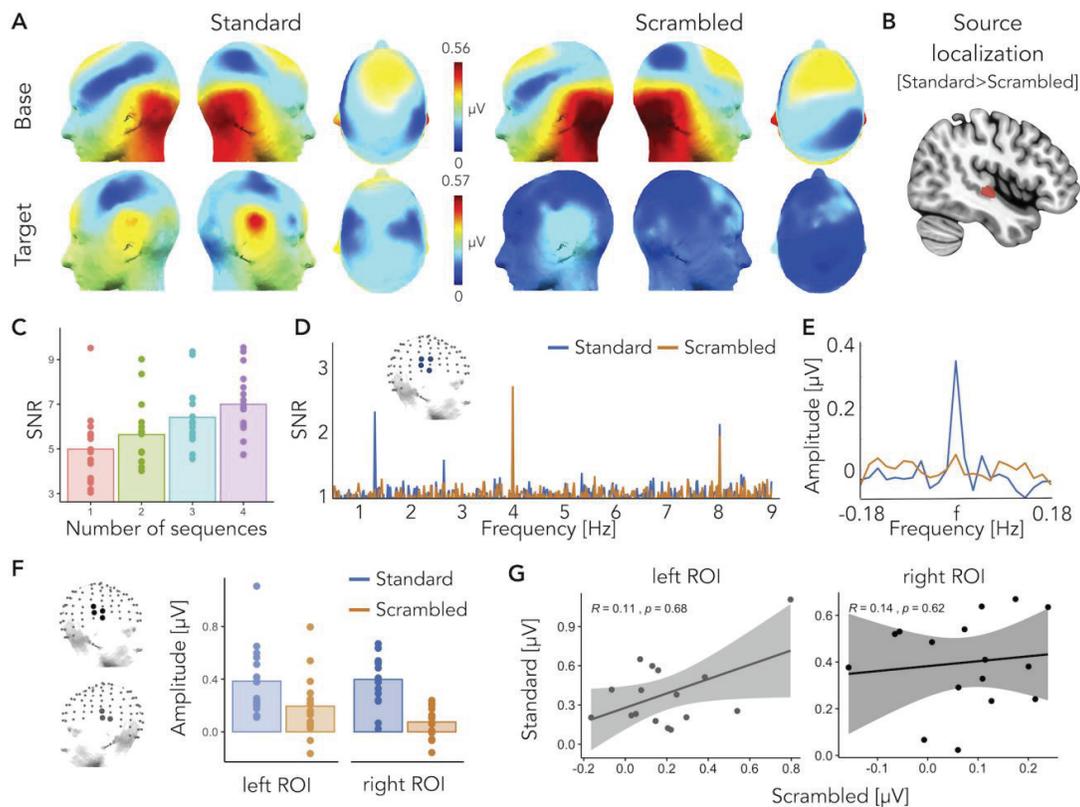
729 Schematic representation of the paradigm. C) Standard and scrambled sequences: Bode magnitude plot

730 expressing the magnitude in decibels as a function of frequency for the averaged sounds of vocal and non-

731 vocal stimuli separately, for standard and scrambled sequences. D) 3 s excerpts of the harmonic sequence

732 (left) with its spectrogram (right). E) Acoustic features as a function of sound category: harmonicity-to-

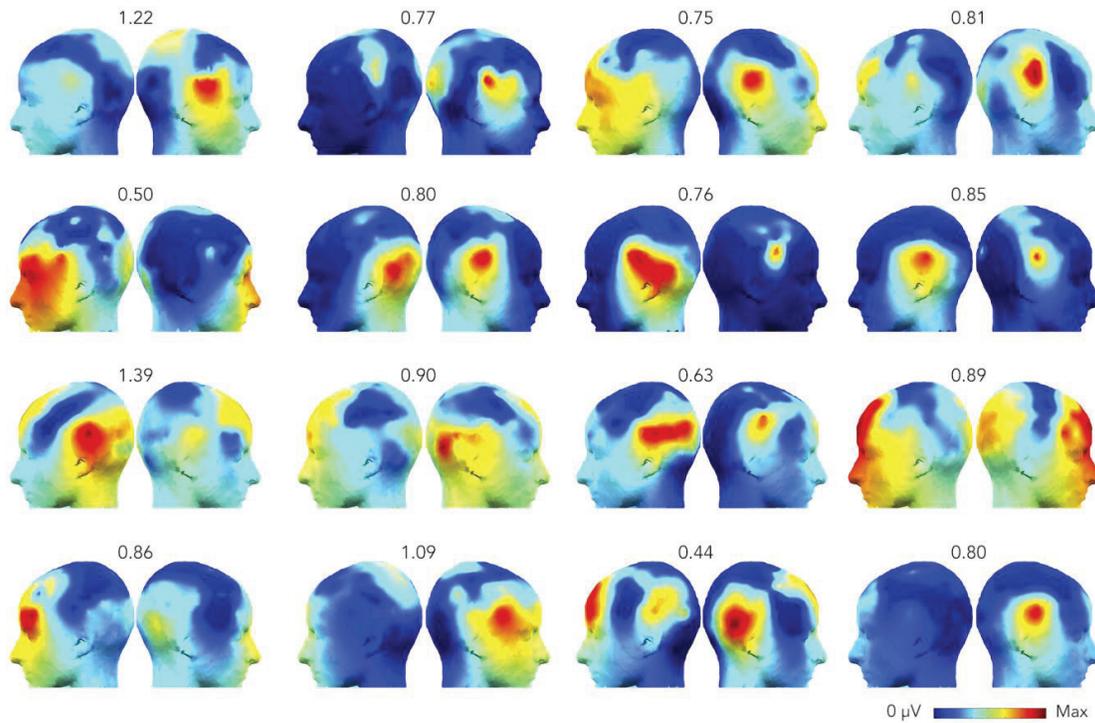
733 noise ratio, pitch and spectral center of gravity.



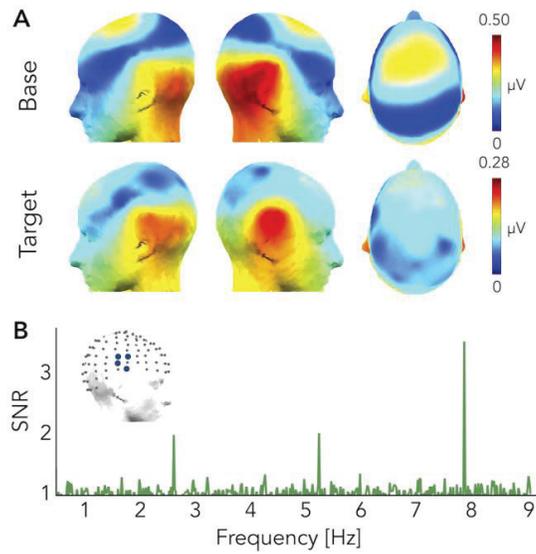
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735 **Figure 2. Experiment 1 – Voice versus object sounds.** A) Responses at the base (top) and at the target  
 736 frequency (bottom) for the standard (left) and scrambled (right) conditions as topographic head plots.  
 737 Topographic head plots were obtained by summing the baseline subtracted amplitude at the significant  
 738 harmonics. B) Source localization analysis revealed stronger coherence values at the target frequency for  
 739 the standard condition (standard > scrambled) over right superior and middle temporal areas (voxels with  
 740 intensity above the 95<sup>th</sup> percentile are highlighted in red). C) Signal-to-noise ratio (SNR) of voice-selective  
 741 responses obtained by averaging SNR values of ROIvoice electrodes as a function of number of stimulation  
 742 sequences/minutes of recording for the standard condition. D) SNR averaged spectra of ROIvoice  
 743 electrodes. E) Sum of the baseline corrected amplitude (considering 10 bins on each side, excluding the  
 744 immediately adjacent ones) of voice selective responses at the four significant harmonics for the standard  
 745 (blue) and scrambled condition (orange). F) Responses at the target frequency for the standard (blue) and  
 746 scrambled (orange) conditions as the sum of baseline subtracted amplitude at four harmonics in the left

747 and right ROIs. G) There is no correlation between responses at the left and right ROIs across the standard  
748 and scrambled conditions.

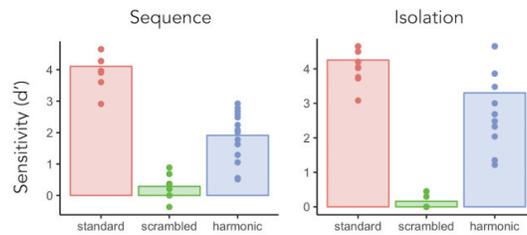


749  
750 **Figure 3. Experiment 1 - individual voice-selective responses.** Responses at the voice presentation  
751 frequency for each individual. Topographic head plots represent the sum of the baseline subtracted  
752 amplitude of significant harmonics as identified at the group level. The scale of each head plot ranges from  
753 0 μV to the maximum (reported on top) for each subject.



754

755 **Figure 4. Experiment 2 – Voice versus musical instruments.** A) Responses at the base and at the target  
 756 frequency as topographic head plots. Topographic head plots were obtained by summing the baseline  
 757 subtracted amplitude at the significant harmonics. B) SNR averaged spectra of ROIvoice electrodes.



758

759 **Figure 5. Experiment 3 - Behavioral detection of voices.** Sensitivity indices for the sequence (left) and  
 760 isolation (right) tasks, for the three conditions. The bar plots represent the group average of  $d'$ , each dot  
 761 represents an individual participant's  $d'$  score.