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1 **Cerebral activity in female baboons (*Papio anubis*) during the perception of conspecific and**  
2 **heterospecific agonistic vocalizations: A functional Near Infrared Spectroscopy study**

3 Debracque, Coralie.<sup>1\*</sup>, Gruber, Thibaud.<sup>1</sup>, Lacoste, Romain.<sup>2</sup>, Meguerditchian, Adrien.<sup>2,3Ψ</sup> &  
4 Grandjean, Didier.<sup>1Ψ</sup>

5  
6 <sup>1</sup>Neuroscience of Emotion and Affective Dynamics Lab, Faculty of Psychology and Educational  
7 Sciences and Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland.

8 <sup>2</sup>Station de Primatologie - Celphedia, CNRS UARS846, Rousset-sur-Arc, France.

9 <sup>3</sup>Laboratoire de Psychologie Cognitive UMR7290, CNRS, Université Aix-Marseille, Marseille, France.

10 <sup>Ψ</sup>joint senior authors

11 \*Correspondence to: [Coralie.Debracque@unige.ch](mailto:Coralie.Debracque@unige.ch); <https://orcid.org/0000-0001-9854-1283>; Swiss  
12 Center for Affective Sciences, Campus Biotech, Chemin des Mines 9, 1202, Geneva, Switzerland.

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29 **Abstract**

30 The “voice areas” in the superior temporal cortex have been identified in both humans and non-human  
31 primates as selective to conspecific vocalizations only (i.e expressed by members of our own species),  
32 suggesting its old evolutionary roots across the primate lineage. With respect to non-human primate  
33 species, it remains unclear whether the listening of vocal emotions from conspecifics leads to similar  
34 or different cerebral activations when compared to heterospecific calls (i.e. expressed by another  
35 primate species) triggered by the same emotion. Using a neuroimaging technique rarely employed in  
36 monkeys so far, functional Near Infrared Spectroscopy, the present study investigated in three lightly  
37 anaesthetised female baboons (*Papio anubis*), temporal cortex activities during exposure to agonistic  
38 vocalizations from conspecifics and from other primates (chimpanzees - *Pan troglodytes*), and energy  
39 matched white noises in order to control for this low-level acoustic feature. Permutation test analyses  
40 on the extracted OxyHemoglobin signal revealed great inter-individual differences on how conspecific  
41 and heterospecific vocal stimuli were processed in baboon brains with a cortical response recorded  
42 either in the right or the left temporal cortex. No difference was found between emotional vocalizations  
43 and their energy matched white noises. Despite the phylogenetic gap between *Homo sapiens* and  
44 African monkeys, modern humans and baboons both showed a highly heterogeneous brain process for  
45 the perception of vocal and emotional stimuli. The results of this study do not excluded that old  
46 evolutionary mechanisms for vocal emotional processing may be shared and inherited from our  
47 common ancestor.

48

49 **Keywords**

50 fNIRS, cerebral activity, monkey, agonistic vocalisations, conspecific, heterospecific

## 51 1. Introduction

52 Since the 1990s (George et al. 1995; Pihan, Altenmüller, and Ackermann 1997), many neuroimaging  
53 studies have investigated the activity of the human temporal cortex during emotional voice processing.  
54 Hence, functional Magnetic Resonance Imaging (fMRI) and more recently functional Near Infrared  
55 Spectroscopy (fNIRS) data pointed out the role of the bilateral superior temporal gyrus (STG), superior  
56 temporal sulcus (STS) and middle temporal gyrus (MTG) in the processing of emotional prosody  
57 (Grandjean 2020; Grandjean et al. 2005, 2005; Kotz et al. 2013; Plichta et al. 2011; Wildgruber et al.  
58 2009; Zatorre and Belin 2001) and more specifically in the recognition of positive and negative  
59 emotions (Bach et al. 2008; Frühholz and Grandjean 2013; Johnstone et al. 2006; Zhang, Zhou, and  
60 Yuan 2018).

61 Despite calls for an evolutionary-based approach to emotions that consider the adaptive functions and  
62 the phylogenetic continuity of emotional expression and identification (Bryant 2021; Greenberg 2002),  
63 few comparative studies have investigated the human temporal cortex activity during the recognition of  
64 emotional cues in human voices (conspecific) and other species vocalizations (heterospecific),  
65 expressed especially by non-human primates (NHP), our closest relatives (Perelman et al. 2011). In the  
66 few studies published so far, fMRI conjunction analysis has interestingly identified commonalities in  
67 the human cerebral response to human and other animal vocalizations including macaques (*Macaca*  
68 *mulatta*) and domestic cats (*Felis catus*). More activations were indeed found in the medial posterior  
69 part of the human right orbitofrontal cortex (OFC) during the listening of agonistic vocalizations  
70 expressed by both humans and other animals compared to affiliative ones (Belin et al. 2008). On the  
71 contrary, Fritz and colleagues demonstrated a greater involvement of the human STS and the right  
72 planum temporale (PT) for the identification of human emotional voices contrasted to chimpanzee (*Pan*  
73 *troglodytes*) and then macaques calls (Fritz et al. 2018). Similar results were found in the STS and STG  
74 when human emotional voices were compared to various animal sounds, non-vocal stimuli or non-  
75 biological noises (Bodin et al. 2021; Pernet et al. 2015) suggesting a sensitivity of the superior regions  
76 of the human temporal cortex but not of the frontal cortex for conspecific voices.

77 Is this sensitivity of the temporal cortex to emotional cues expressed by conspecifics found in NHP? In  
78 other words, are the cerebral mechanisms of vocal emotion perception shared across primate species,  
79 or has the auditory cortex of *Homo sapiens* evolved differently?

80 The previous literature on primates emphasizes brain continuity between humans and NHP for the  
81 auditory processing of conspecific emotions. For instance, fMRI studies in macaques have revealed a  
82 greater involvement of the STG for the perception of conspecific emotional calls compared to  
83 heterospecific ones including calls from other primate and non-primate species, environmental sounds  
84 and scrambled vocalizations (Joly et al. 2012; Ortiz-Rios et al. 2015; Petkov et al. 2008). Following  
85 this, positron emission tomography (PET scan) studies have shown the predominant role of the right  
86 PT in chimpanzees (Tagliabattola et al. 2009) and of the STS in macaques (Gil-da-Costa et al. 2004) for

87 the processing of conspecific emotional calls. Additionally, neurobiological findings in macaques and  
88 marmosets (*Callithrix jacchus*) have suggested a greater involvement of the STG and of the primary  
89 auditory cortex in the passive listening of emotional conspecific calls compared to environmental  
90 sounds, scrambled or time-reversed vocalizations (Belin 2006; Ghazanfar and Hauser 2001; Poremba  
91 et al. 2004). Overall, as for humans, the literature in NHP suggests a sensitivity of the great ape and  
92 monkey temporal cortex for the processing of conspecific emotional vocalizations.

93 Despite these results, the question of the specific status of conspecific emotions in NHP remains poorly  
94 explored with respect to heterospecific vocalizations. In particular, because of the species-dependent  
95 results in humans highlighted above and the phylogenetic proximity across primate species, it seems  
96 necessary to include heterospecific stimuli from other NHP to reconstruct the phylogenetic evolution  
97 of primate vocal emotion processing (Bryant 2021).

98 The present study investigated temporal cortex involvement in three female baboons: Talma, Rubis and  
99 Chet, during exposure to conspecific vs. heterospecific agonistic vocalizations, using fNIRS. Building  
100 on a growing interest over the past decade (Boas et al. 2014; Pan, Borragán, and Peigneux 2019), we  
101 used fNIRS because of its non-invasiveness, its poor sensitivity to motion artefacts (Balardin et al.  
102 2017) and its suitability for comparative research (Debracque et al. 2021; Fuster et al. 2005; Kim et al.  
103 2017; Lee et al. 2017; Wakita et al. 2010). According to the existing literature on NHP and humans  
104 suggesting a sensitivity of the primates' temporal cortex for conspecific calls, we expected *i*) more  
105 activation in the temporal cortex for the passive listening of baboon sounds compared to chimpanzee  
106 stimuli; and *ii*) a greater involvement of the temporal cortex for the perception of agonistic conspecific  
107 vocalizations in comparison to the other sounds.

108

## 109 **2. Material & Methods**

### 110 **2.1. Subjects**

111 The few existing studies using fNIRS in NHP mostly include a single subject (Fuster et al. 2005; Wakita  
112 et al. 2010). Three healthy female baboons (Talma – 13.5 years old; Rubis – 18.4 years old; and Chet –  
113 11.8 years old) were included in the present study, contingent with their yearly health check-up; this  
114 sample size was consistent with prior work on the perception of affective stimuli by female macaques  
115 (Lee et al. 2017). In addition, as male baboons have large and thick masticatory muscles above their  
116 temporal cortex, they were excluded from the experimental protocol. Sexual dimorphism being  
117 particularly pronounced in baboons (Phillips-Conroy and Jolly 1981), the female sex was assigned to  
118 the subjects based on their facial morphology and red buttocks. Moreover, preventing any ambiguity  
119 about the subjects' sex, the three female baboons had already given birth to offspring that they breastfed.  
120 Following this, based on the annual health assessment and the daily behavioural surveys made by the  
121 veterinary and animal welfare staff, the subjects had normal hearing abilities and did not present a

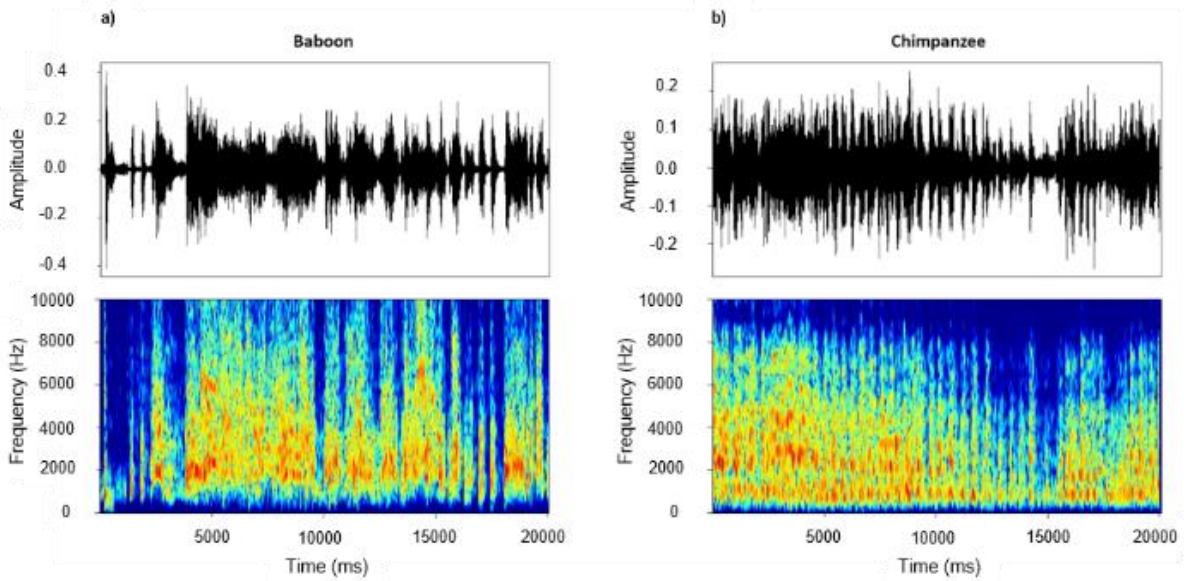
122 structural neurological impairment (confirmed with respective T1w anatomical brain images – 0.7 x 0.7  
123 x 0.7 resolution – collected in vivo under anesthesia in the 3Tesla MRI Brunker machine). All  
124 procedures were approved by the “C2EA -71 Ethical Committee of neurosciences” (INT Marseille) and  
125 performed in accordance with the relevant French law, CNRS guidelines and the European Union  
126 regulations. The subjects were born in captivity and housed in social groups at the Station de  
127 Primatologie in which they have free access to both outdoor and indoor areas. All enclosures are  
128 enriched by wooden and metallic climbing structures as well as substrate on the group to favour foraging  
129 behaviours. Water is available *ad libitum* and monkey pellets, seeds, fresh fruits and vegetables were  
130 given every day. The three subjects were lightly anesthetized with propofol and passively exposed to  
131 auditory stimuli as described below (see also Debracque et al. 2021 for the complete protocol).

## 132 **2.2. Stimuli**

133 Auditory stimulations consisted of agonistic vocalizations produced by baboon (conspecific – see  
134 Figure 1a) and chimpanzee (heterospecific – see Figure 1b) individuals as well as energy matched white  
135 noises to control for this low-level acoustic feature and for its unfolding (i.e. the temporal structure of  
136 energy of the vocalizations). Aggressor screams and distress calls expressed in an agonistic (i.e.  
137 conflictual) context are commonly used in the literature to investigate affective states associated with  
138 threat and distress respectively in primate vocalizations (Briefer 2012; Kret et al. 2020). More  
139 specifically, studies on the baboons’ vocal repertoire have shown the link between agonistic  
140 vocalizations produced during conflicts and the threatening or distressful emotional state of the caller  
141 (Kemp et al. 2017; Seyfarth and Cheney 2009).

142 Each auditory stimulus had a duration of 20 seconds, and was repeated six times (see Debracque et al.  
143 2021 for more details). The auditory stimuli were pseudo-randomized, alternating vocalizations and  
144 white noises; and were separated by 15 seconds of silence. Additionally, auditory stimulations were  
145 broadcasted either binaurally or monaurally in the right or left ear.

146



147

148 **Figure 1:** Representative waveforms and spectrograms of 20s-long agonistic **a)** baboon and **b)**  
 149 chimpanzee vocalizations used as stimuli in the present study. These graphical representations were  
 150 extracted using the PhonTools package (Barreda 2015) on R. studio (Team 2020).

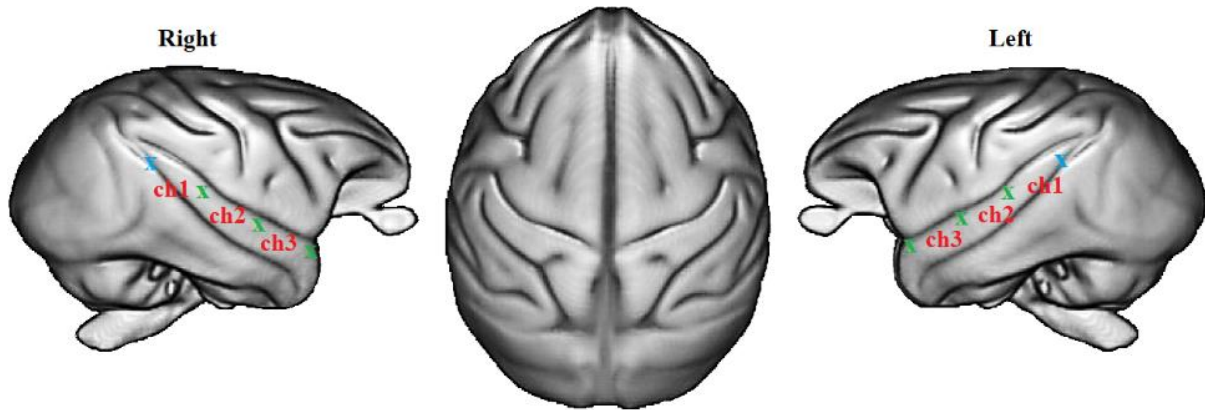
## 151 2.3. fNIRS

### 152 2.3.1. Recordings

153 Brain activations were measured using two light and wireless fNIRS devices (Portalite, Artinis Medical  
 154 Systems B.V., Elst, The Netherlands). Based on tissue transillumination (Bright 1831), fNIRS measures  
 155 using near infrared lights blood oxygenation changes (e.g. Hoshi 2016; Jöbsis 1977) related to the  
 156 hemodynamic response function constituted of Oxyhemoglobin (O<sub>2</sub>Hb) and deoxyhemoglobin. fNIRS  
 157 is a non-invasive technique poorly sensitive to motion artefacts (Balardin et al. 2017) and fully  
 158 wearable. The fNIRS optical probes were placed on the right and left temporal cortices of the subjects  
 159 using T1 MRI scanner images previously acquired at the Station de Primatologie on baboons (see Figure  
 160 2). Data were obtained at 50 Hz with two wavelengths (760 and 850 nm) using three measurement, i.e.  
 161 channels per hemisphere (ch1, ch2, ch3) with three inter-distance probes (3 – 3.5 – 4 cm) investigating  
 162 three different cortical depths (1.5 – 1.7 – 2 cm respectively).

163 Reducing the potential disturbing impact of the fNIRS protocol on the subjects, each experimental  
 164 session was planned during the baboons' routine health inspection at the Station de Primatologie. As  
 165 part of the health check, subjects were isolated from their social group and anesthetized with an  
 166 intramuscular injection of ketamine (5 mg/kg - Ketamine 1000®) and medetomidine (50µg/kg -  
 167 Domitor®). Then Sevoflurane (Sevotek®) at 3 to 5% and atipamezole (250 µg/kg - Antisedan®) were  
 168 administered before recordings. Each baboon was placed in ventral decubitus position on the table and  
 169 the head of the individual was maintained using foam positioners, cushions and Velcro strips to remain  
 170 straight and to reduce potential motion occurrences. Vital functions were monitored (SpO<sub>2</sub>, Respiratory

171 rate, ECG, EtCO<sub>2</sub>, T°) and a drip of NaCl was put in place during the entire anaesthesia. Before fNIRS  
172 recordings, temporal areas on the baboons' scalp were shaved and sevoflurane inhalation was stopped.  
173 Subjects were further sedated with a minimal amount of intravenous injection of Propofol (Propovent®)  
174 with a bolus of around 2mg/kg every 10 to 15 minutes or by infusion rate of 0.1 – 0.4 mg/kg/min. After  
175 the recovery period, subjects were put back in their social group and monitored by the veterinary staff.  
176



177  
178 **Figure 2:** fNIRS optode and channel locations according to 89 baboons T1 MRI template (Love et al.  
179 2016). Blue and green crosses represent optical receivers and transmitters respectively. Ch1, Ch2 and  
180 Ch3 indicate the three channels on the right and left temporal cortex.

### 181 2.3.2. Analysis

182 SPM\_fNIRS toolbox (Tak et al. 2016) and custom made codes on Matlab 7.4 R2009b (The MathWorks  
183 Inc. 2009) were used to perform first level analysis on raw fNIRS data following this procedure:

184 *i)* O<sub>2</sub>Hb concentration changes were calculated using the Beer-Lambert law (Delpy et al. 1988); *ii)*  
185 motion artifacts were removed manually in each individual and each channel. In total, 10 seconds  
186 (1.3%) were removed from the O<sub>2</sub>Hb signal of Rubis and 35 seconds (4.8%) for Talma and Chet; *iii)* a  
187 low-pass filter based on the HRF (Friston et al. 2000) was applied to reduce physiological confounds;  
188 *iv)* a baseline correction was applied in subtracting the pre-stimulus baseline from the post-stimulus  
189 O<sub>2</sub>Hb concentration changes of each trial and *v)* O<sub>2</sub>Hb signal was averaged for Talma in a window of  
190 4 to 12 s post stimulus onset for each trial; and for Rubis and Chet in a window of 2 to 8 s post stimulus  
191 onset in order to select the range of maximum O<sub>2</sub>Hb concentration changes following Debracque et al  
192 2021. Shortly, the differences of concentration range are explained by the presence of tachycardia  
193 episodes for both Rubis and Chet during the experiment, involving an HRF almost twice as fast as the  
194 one found for Talma.

195 The second level analysis was made on R. studio (Team 2020) using the permuco package (Frossard  
196 and Renaud 2019). Through the same data sample, we already demonstrated in Debracque et al., 2021,  
197 the robustness of our method and results regarding hemispheric lateralization following motor and  
198 auditory stimulations. In the present paper, we wanted to investigate a higher level of brain process, i.e.



199 the perception of conspecific and heterospecific sounds. Hence, in each *Hemisphere* (right, left), we  
200 used non-parametric permutation tests with 5000 iterations to assess O<sub>2</sub>Hb concentration changes for  
201 each subject (Talma, Rubis, Chet) as they enable repeated measures ANOVA in small sample sizes by  
202 multiplying the design and response variables (Kherad-Pajouh and Renaud 2015). *Stimuli* (call, white  
203 noise); *Species* (baboon, chimpanzee); *Channels* (ch1, ch2, ch3) and *Stimulus sides* (right, left, both  
204 ears) were selected as fixed factors. As recommended, contrast effects of *Species* and *Stimuli* within  
205 channels were assessed with 2000 permutations (Kherad-Pajouh and Renaud 2015). Both p. values for  
206 permutation  $F$  ( $p_{\text{perm}}$ ) and parametric  $F$  are reported.

### 207 3. Results

208 First, regarding the subject Talma, permutation tests revealed significant differences of O<sub>2</sub>Hb  
209 concentration changes between the three *Channels* for the right ( $F(2,3) = 161.5$ ,  $p | p_{\text{perm}} < .001$ ) and  
210 left hemisphere ( $F(2,3) = 33.91$ ,  $p | p_{\text{perm}} < .001$ ). The main factor *Species* was also found significant  
211 for the left hemisphere only (right:  $F(1,2) = 0.34$ ,  $p | p_{\text{perm}} = .057$ ; left:  $F(1,2) = 4.24$ ,  $p | p_{\text{perm}} < .05$ ). The  
212 main factor *Stimuli* as well as the interactions *Stimuli\*Species*, *Stimuli\*Channels*, *Species\*Channels*  
213 and *Stimuli\*Species\*Channels* did not reach significance within the right or left hemisphere (see  
214 Supplementary Material). Following these analyses, contrasts within each channel showed that for  
215 Talma's left hemisphere, the perception of baboon sounds led to lower O<sub>2</sub>Hb concentration changes  
216 compared to chimpanzee sounds in ch1, ch2 and ch3 (right:  $F(1,2) = 0.15$ ,  $p | p_{\text{perm}} = .69$ ; left:  $F(1,2) =$   
217  $4.07$ ,  $p | p_{\text{perm}} = .05$  - see Figure 3a).

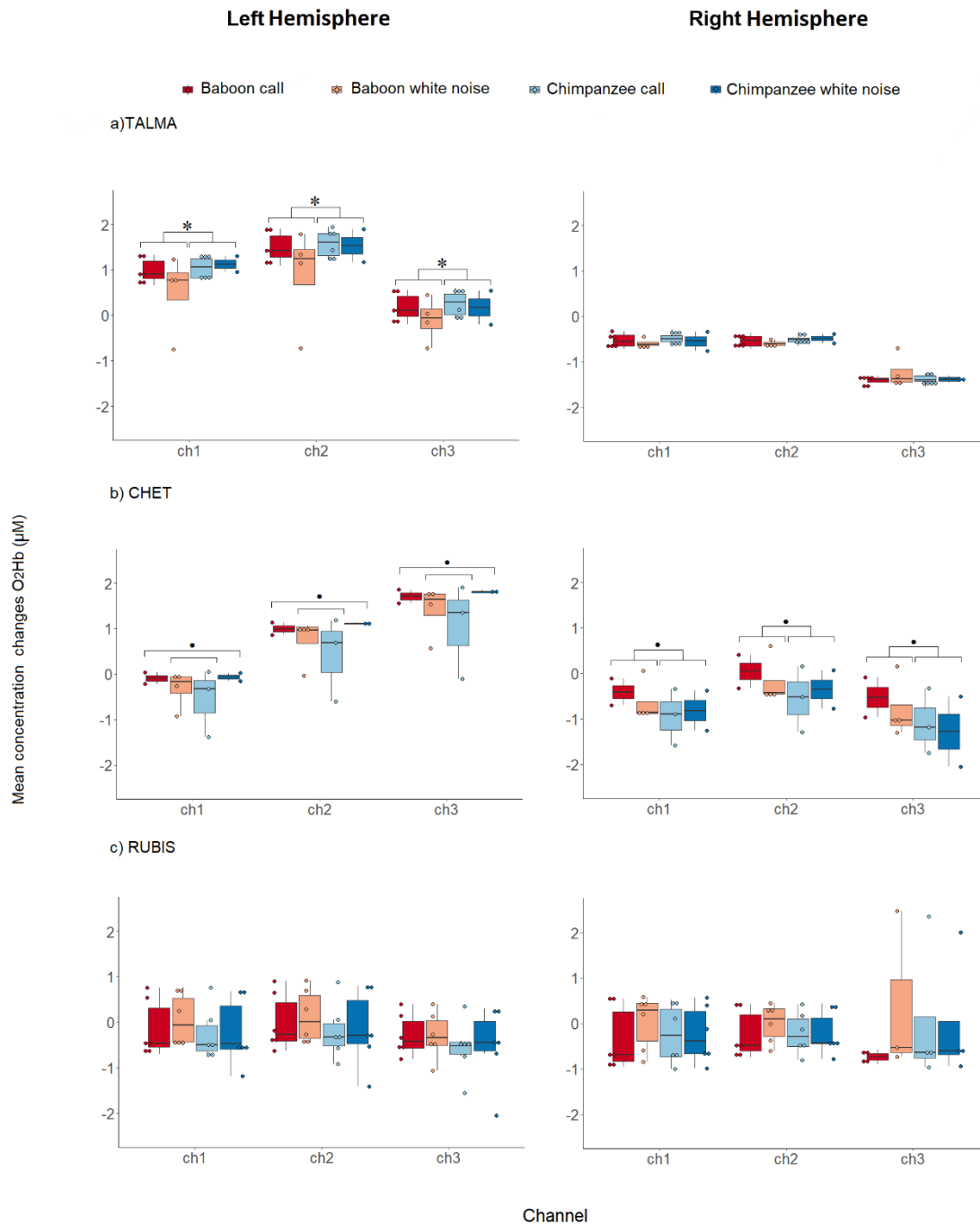
218 Second, for the subject Chet, significant differences of O<sub>2</sub>Hb concentration changes between the three  
219 *Channels* were found for the right (right:  $F(2,3) = 3,99$ ,  $p | p_{\text{perm}} < .05$ ) and left hemisphere ( $F(2,3) =$   
220  $25.68$ ,  $p | p_{\text{perm}} < .001$ ). The main factor *Species* was also found significant for the right hemisphere only  
221 (right:  $F(1,2) = 5.03$ ,  $p | p_{\text{perm}} < .05$ ; left:  $F(1,2) = 0.24$ ,  $p | p_{\text{perm}} = .62$ ). Additionally, statistics showed a  
222 significant two-way interaction between *Stimuli* and *Species* for the left hemisphere only (right:  $F(1,2)$   
223  $= 0.01$ ,  $p | p_{\text{perm}} = 1$ ; left:  $F(1,2) = 4.13$ ,  $p | p_{\text{perm}} = .05$ ). The main factor *Stimuli* as well as the interactions  
224 *Stimuli\*Channels*, *Species\*Channels* and *Stimuli\*Species\*Channels* did not reach significance within  
225 the right or left hemisphere (see Supplementary Material). Finally, contrasts within each channel  
226 revealed that for Chet, while her right hemisphere had a tendency to be more activated for the perception  
227 of baboon sounds compared to chimpanzee stimuli in ch1, ch2 and ch3 (right:  $F(1,2) = 3.74$ ,  $p | p_{\text{perm}}$   
228  $= .07$ ; left:  $F(1,2) = 0.22$ ,  $p | p_{\text{perm}} = .65$ ); her left hemisphere had a tendency to be more activated for  
229 the passive listening of baboon agonistic calls and chimpanzee white noises when compared to baboon  
230 white noises and chimpanzee agonistic calls in ch1, ch2 and ch3 (right:  $F(1,2) = 0.01$ ,  $p | p_{\text{perm}} = 1$ ; left:  
231  $F(1,2) = 3.75$ ,  $p | p_{\text{perm}} = .07$  - see Figure 3b).

232 Third, for the subject Rubis, only a significant difference of O<sub>2</sub>Hb concentration changes between the  
233 three *Channels* was found for the right hemisphere (right:  $F(2,3) = 8,99$ ,  $p | p_{\text{perm}} < .001$ ; left:  $F(2,3) =$

234 2.15 ,  $p | p_{perm} = .12$  - see Figure 3c). None of the other main effects or interactions reached significance  
235 within the left or right hemisphere (see Supplementary material).

236 Note that for Talma, Rubis and Chet, the factor *Stimulus sides* (sounds broadcasted either binaurally or  
237 monaurally in the right or left ear) did not reach significance and thus, do not statistically explain  
238 differences in O<sub>2</sub>Hb concentration changes underpinning the perception of baboon and chimpanzee  
239 sounds by our three subjects (see Debracque et al. 2021 for more details related to auditory  
240 asymmetries).

241 In sum, across the three channels, more O<sub>2</sub>Hb concentration changes were found in Talma's left  
242 temporal cortex for the perception of chimpanzee sounds compared to baboon stimuli. Conversely, for  
243 Chet, permutation analyses revealed more O<sub>2</sub>Hb concentration changes in the right temporal cortex for  
244 the passive listening of baboon sounds, especially baboon agonistic calls comparing to chimpanzee  
245 stimuli. Additionally, her left temporal cortex was more activated by baboon agonistic calls and  
246 chimpanzee white noises than for chimpanzee agonistic calls and baboon white noises. For Rubis, the  
247 perception of baboon and chimpanzee sounds did not affect the O<sub>2</sub>Hb concentration changes of her  
248 bilateral temporal cortex. Finally, to the exception of Rubis' left hemisphere, the different cortical  
249 depths of the channels (1.5 – 1.7 – 2 cm) had an impact on the O<sub>2</sub>Hb measurement of Talma, Chet and  
250 Rubis' temporal cortices.



251

252 **Figure 3:** Right and left temporal cortex activations for the baboons **a) Talma**, **b) Chet** and **c) Rubis**  
 253 during the perception of agonistic baboon (conspecific) and chimpanzee (heterospecific) vocalizations  
 254 as well as their energy matched white noises. The mean concentration changes of O<sub>2</sub>Hb (y axis) are  
 255 represented in micro molar (µM) for each fNIRS channel (x axis). Colourful dots and dark lines  
 256 represent stimuli and confidence intervals respectively. Results of the permutation tests within channels  
 257 are shown with \* p<.05; \*\* p<.01. The ggplot2 package (Wickham et al. 2021) on R.studio (Team 2020)  
 258 was used for visualizing the data.

259

#### 260 4. Discussion

261 The present fNIRS study in baboons underlines a highly heterogeneous process for the auditory  
262 perception of conspecific and heterospecific affective stimuli.

263 Using valid statistical methods and analyses (Debracque et al. 2021; Lee et al. 2017) as well as the  
264 inclusion of three subjects instead of one, as is usually the case in the relevant literature (Fuster et al.  
265 2005; Wakita et al. 2010), fNIRS data revealed large inter-individual differences between Talma and  
266 Chet for the significant main effect *Species*. The left temporal cortex of Talma was overall more  
267 activated for chimpanzee sounds (calls and white noise) than for baboon ones; in contrast, results were  
268 reversed in the right temporal cortex of Chet, where statistical analyses highlighted an increase of O<sub>2</sub>Hb  
269 concentration changes for the passive listening of agonistic baboon sounds, especially baboon agonistic  
270 calls compared to chimpanzee sounds. In addition, in her left temporal cortex, we documented an  
271 increase in O<sub>2</sub>Hb concentration led by both the perception of agonistic baboon calls and chimpanzee  
272 white noises. No significant results were found for Rubis, although this may have been a consequence  
273 of her constant tachycardia during the health check and experiment (see Debracque et al. 2021).

274 Beyond this apparent absence of congruence in our fNIRS data, our results underlined in fact a highly  
275 heterogeneous process for auditory perception in baboons. Well-known in neuroscience research with  
276 human participants, inter-individual differences are for instance at play in the location of voice selective  
277 areas in human auditory cortex (Belin et al. 2000). In the same line, Pernet and colleagues also  
278 demonstrated using fMRI, a great inter-individual variability in the involvement of human STG and  
279 STS for the listening of conspecific emotional voices compared to non-vocal sounds (Pernet et al. 2015).  
280 As for humans, the location of the voice selective areas as well as the cortical response of the superior  
281 temporal cortex in baboons would be subject to a high heterogeneity. This claim is in line with the  
282 results of Xu and colleagues (2019) who have shown in five anaesthetized and awake macaques great  
283 inter-individual variabilities in the functional connectivity of different cortical regions (Xu et al. 2019).  
284 Interestingly, the authors compared macaques' fMRI data to human ones and concluded on a similar  
285 heterogeneity in functional connectivity across primate species. As highly cited human neuroimaging  
286 studies (Szucs and Ioannidis 2020), future non-invasive comparative research should include more  
287 subjects to take in consideration this inter-individual variability in brain mechanisms. The necessity to  
288 increase NHP subjects to address limits in statistical power faces ethical aspects related to animal  
289 welfare in the case of invasive neuroimaging studies. The development of fNIRS (Debracque et al.  
290 2021) and longitudinal studies in comparative neuroscience (Song et al. 2021) would thus allow  
291 answering parts of these challenges.

292 Often explored using fMRI or Pet scan (e.g. Bodin et al. 2021; Gil-da-Costa et al. 2004; Ortiz-Rios et  
293 al. 2015), our fNIRS data remain however inconclusive regarding the processing of conspecific  
294 vocalizations compared to white noises. In contrast, comparative research on macaques and marmoset

295 (*Callithrix jacchus*) showed a greater sensitivity of the temporal cortex in its anterior part than in its  
296 posterior area for the contrast conspecific calls vs. control sounds (Bodin et al. 2021). Future fNIRS  
297 studies would help determinate whether this lack of effect replication from our present study might be  
298 addressed by improving the probe location on the scalp of baboons and its spatial sensitiveness to this  
299 expected effect.

300 Finally, out of the scope of this paper, permutation test analyses highlighted consistent fNIRS data for  
301 the channels 1 and 2 compared to channel 3 on both, right and left hemispheres. This result suggests  
302 that, for fNIRS in baboons, the best inter-probe distant to assess cortical activations in temporal cortex  
303 would be between 3cm and 3.5cm. Interestingly, these distances are commonly used for fNIRS  
304 experiments in human adults (Ferrari and Quaresima 2012).

305 To conclude, our fNIRS data mainly pointed out the existence of a highly heterogonous process across  
306 individuals for the perception of conspecifics emotional vocalizations in baboons. Whereas such an  
307 inter-individual heterogeneity is also well documented in humans, we do thus not excluded a potential  
308 phylogenetic continuity with non-human primates in the brain processing of conspecific emotional  
309 vocalizations which might be inherited from our common ancestor. Our results remain however  
310 inconclusive, notably in regards to the lack of contrasts conspecific agonistic vocalizations vs. white  
311 noises (control sounds), which are often explored meaningfully using fMRI or Pet scan (e.g. Bodin et  
312 al. 2021; Gil-da-Costa et al. 2004; Ortiz-Rios et al. 2015). This highlights one of the limitations of our  
313 study. fNIRS, Pet scan and fMRI measure hemodynamic changes, however the later have a much higher  
314 spatial resolution (Gosseries et al. 2008) than fNIRS (Scholkmann et al. 2014). Secondly, another  
315 limitation is that our experiment focused on baboons and it is unclear whether it will replicate in other  
316 NHP species such as Americas' monkeys. In fact, Fitch and Braccini (2013) have already suggested  
317 differences between monkeys in terms of mechanisms for the processing of conspecific and  
318 heterospecific vocalizations (Fitch and Braccini 2013). A final limitation of our study is that only  
319 agonistic vocalizations were included in the present fNIRS protocol. Similarly to humans, NHP might  
320 have some distinctive brain mechanisms for negative and positive emotions (e.g. Davidson 1992;  
321 Frühholz and Grandjean 2013; Zhang et al. 2018).

322 Overall, our study does not exclude the existence of common evolutionary roots for auditory processing  
323 across primate species to explain the inter-individual variability generally reported in those studies and  
324 underlines the importance of comparative research in monkeys to understand brain mechanisms at play  
325 in modern humans.

326

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#### 339 *Conflict of interest*

340 The authors have no conflicts of interest to declare that are relevant to the content of this article.

#### 341 *Availability of data and material*

342 Raw data are freely available to any researcher.

#### 343 *Code availability*

344 Custom Matlab and R. studio codes are available on request.

#### 345 *Ethics approval*

346 All animal procedures were approved by the “C2EA -71 Ethical Committee of neurosciences” (INT  
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#### 352 *Consent to participate*

353 Not applicable.

#### 354 *Consent for publication*

355 Not applicable.

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