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Cerebral activity in monkeys *Papio anubis* during the perception of conspecific and heterospecific agonistic vocalizations: A functional Near Infrared Spectroscopy study

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29 **Abstract**

30 Are conspecific emotional vocalizations special? Although often investigated in non-human primates
31 using functional magnetic resonance imaging or positron emission tomography, it remains unclear
32 whether the listening of conspecific vocal emotions leads to similar or different cerebral activations
33 when compared to heterospecific calls (i.e. expressed by another primate species). Using a
34 neuroimaging technique rarely employed in monkeys so far, functional Near Infrared Spectroscopy
35 (fNIRS), the present study investigated cortical temporal activities during exposure to both conspecific
36 and heterospecific calls in three female adult baboons (*Papio anubis*). The three subjects were lightly
37 anesthetized and passively exposed to agonistic baboon and chimpanzee (*Pan troglodytes*)
38 vocalizations, as well as energy matched white noises in order to control for this low-level acoustic
39 feature. Despite inter-individual variabilities, permutation test analyses on the extracted
40 OxyHemoglobin signal revealed for two subjects out of three significant differences between the
41 passive listening of baboon *versus* chimpanzee stimuli. Additionally, in one subject, a modulation of
42 the left temporal cortex activity was found for the perception of baboon calls contrasted to chimpanzee
43 vocalizations as well as for the passive listening of baboon white noises compared to chimpanzee ones.
44 Although the lack of generalization of those findings in all three subjects prevents us to draw any
45 conclusion and that more subjects would be needed, the hypothesis that baboons' cortical temporal
46 regions may be more sensitive to the processing of conspecific sounds compared to heterospecific
47 stimuli is not excluded. Our study highlights that fNIRS may be a promising alternative to further
48 investigate the auditory mechanisms at play in the right and left baboons' temporal cortices for the
49 processing of emotional vocalizations.

50 **Keywords**

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

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61 1. Introduction

62 Since the 1990s (George et al. 1995; Pihan, Altenmüller, and Ackermann 1997), many neuroimaging
63 studies have investigated the human temporal cortex activity in emotional voice processing. Hence,
64 functional Magnetic Resonance Imaging (fMRI) and more recently functional Near Infrared
65 Spectroscopy (fNIRS) data pointed out the role of the bilateral superior temporal gyrus (STG), superior
66 temporal sulcus (STS) and middle temporal gyrus (MTG) in the processing of emotional prosody
67 (Grandjean 2020; Grandjean et al. 2005, 2005; Kotz et al. 2013; Plichta et al. 2011; Wildgruber et al.
68 2009; Zatorre and Belin 2001) and more specifically in the recognition of positive and negative
69 emotions (Bach et al. 2008; Frühholz and Grandjean 2013; Johnstone et al. 2006; Zhang, Zhou, and
70 Yuan 2018).

71 Yet, despite calls for an evolutionary-based approach to emotions that consider the adaptive functions
72 and the phylogenetic continuity of emotional expression and identification (Bryant 2021; Greenberg
73 2002), few comparative research investigated the human temporal cortex activity during the recognition
74 of emotional cues in human voices (conspecific) and other species vocalizations (heterospecific),
75 expressed especially by non-human primates (NHP), our closest relative (Perelman et al. 2011). In the
76 few studies published so far, fMRI analysis has revealed more activations in human auditory cortex for
77 the recognition of agonistic vocalizations expressed by humans as well as macaques (*Macaca mulatta*)
78 and domestic cats (*Felis catus*) comparing to affiliative ones. This result was largely driven by a
79 decrease of activity in auditory cortex during the listening of macaque and cat vocalizations compared
80 to human vocalizations (Belin et al. 2008). Additionally, Fritz and colleagues demonstrated a greater
81 involvement of the human STS and the right planum temporale (PT) for the identification of human
82 emotional voices contrasted to chimpanzee (*Pan troglodytes*) and then macaques calls (Fritz et al.
83 2018). Interestingly, similar results were found in the STS and STG when human emotional voices were
84 compared to various animal sounds, non-vocal stimuli or non-biological noises (Bodin et al. 2021;
85 Pernet et al. 2015) suggesting a specific sensitivity of the superior regions of the human temporal cortex
86 for conspecific voices.

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

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

97 processing of conspecific emotional calls. Additionally, neurobiological findings in macaques and
98 marmosets (*Callitrix jacchus*) have suggested a greater involvement of the STG and of the primary
99 auditory cortex in the passive listening of emotional conspecific calls comparing to environmental
100 sounds, scrambled or time-reversed vocalizations (Belin 2006; Ghazanfar and Hauser 2001; Poremba
101 et al. 2004). Despite these results, the question on the specific status of conspecific emotions in NHP
102 remains poorly explored with respect to heterospecific vocalizations. In particular, because of the
103 species-dependent results in humans highlighted above and the phylogenetic proximity across primate
104 species, it seems necessary to include heterospecific stimuli from other NHP to reconstruct the
105 phylogenetic evolution of primate vocal emotion processing (Bryant 2021).

106 The present study investigated temporal cortex involvement in three female baboons: Talma, Rubis and
107 Chet, during exposure to conspecific vs. heterospecific affective vocalizations, using fNIRS. Building
108 on a growing interest over the past decade (Boas et al. 2014; Pan, Borragán, and Peigneux 2019), we
109 used fNIRS because of its non-invasiveness, its poor sensitivity to motion artefacts (Balardin et al.
110 2017) and its suitability for comparative research (Debracque et al. 2021; Fuster et al. 2005; Kim et al.
111 2017; Lee et al. 2017; Wakita et al. 2010). According to the existing literature on NHP and humans
112 suggesting a sensitivity of the primates' temporal cortex for conspecific calls, we expected *i*) more
113 activation in the temporal cortex for the passive listening of baboon sounds compared to chimpanzee
114 stimuli; and *ii*) a greater involvement of the temporal cortex for the perception of agonistic conspecific
115 vocalizations in comparison to the other sounds.

116

117 **2. Material & Methods**

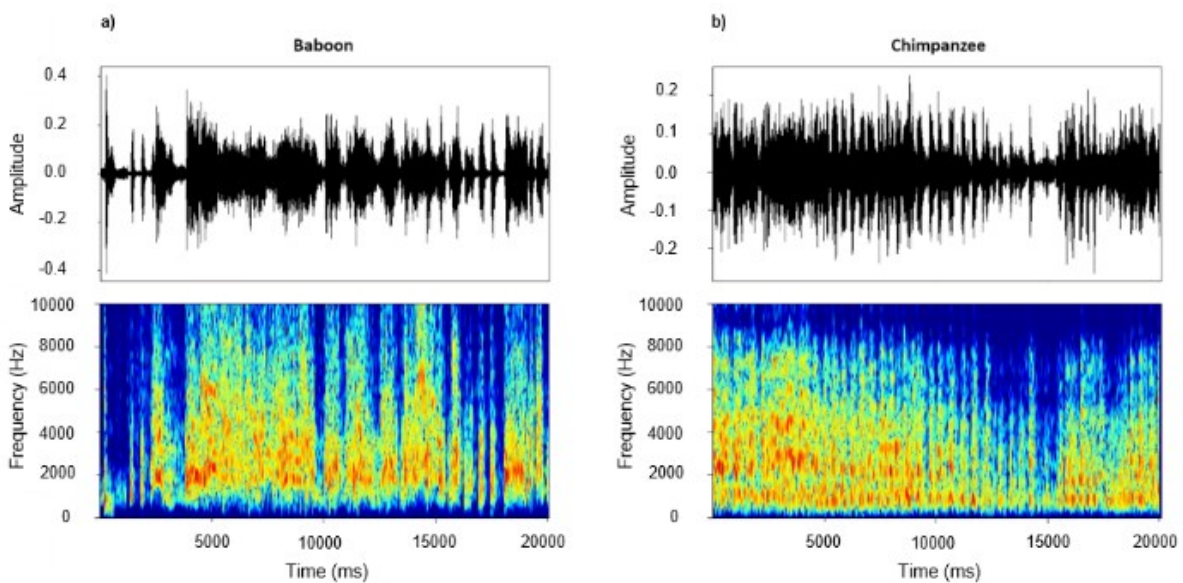
118 **2.1. Subjects**

119 Three healthy female baboons (Talma, Rubis and Chet, mean age = 14.6 years, SD \pm 3.5 years) were
120 included in the present study. Based on the annual health assessment and the daily behavioural surveys
121 made by the veterinary and animal welfare staff, the subjects had normal hearing abilities and did not
122 present a structural neurological impairment (confirmed with respective T1w anatomical brain images
123 – 0.7 x 0.7 x 0.7 resolution – collected in vivo under anesthesia in the 3Tesla MRI Brunker machine).
124 All procedures were approved by the “C2EA -71 Ethical Committee of neurosciences” (INT Marseille)
125 and 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 expressed by baboon (conspecific – see
134 Figure 1a) and chimpanzee (heterospecific – see Figure 1b) species 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). Each stimulus had a duration of 20 seconds, and was repeated six times
137 (see Debracque et al. 2021 for more details). The auditory stimuli were pseudo-randomized, alternating
138 vocalizations and white noises; and were separated by 15 seconds of silence. Additionally, auditory
139 stimulations were broadcasted either binaurally or monaurally in the right or left ear.

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141

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

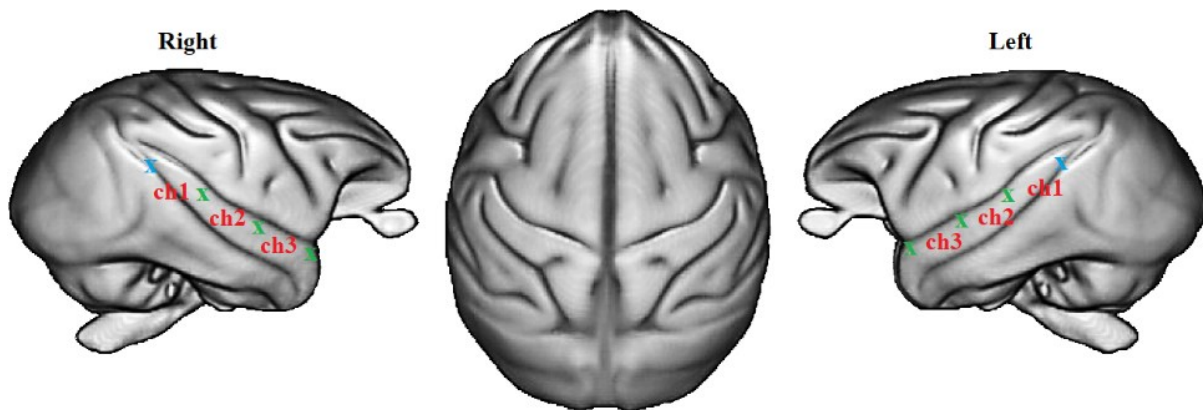
145 2.3. fNIRS

146 2.3.1. Recordings

147 Brain activations were measured using two light and wireless fNIRS devices (Portalite, Artinis Medical
148 Systems B.V., Elst, The Netherlands) enabling the measurement of Oxyhemoglobin (O₂Hb). Optical
149 probes were placed on the right and left temporal cortices of the subjects using T1 MRI scanner images
150 previously acquired at the Station de Primatologie on baboons (see Figure 2). Data were obtained at 50
151 Hz with two wavelengths (760 and 850 nm) using three channels per hemisphere (ch1, ch2, ch3) with
152 three inter-distance probes (3 – 3.5 – 4 cm) investigating three different cortical depths (1.5 – 1.7 – 2
153 cm respectively).

154 Reducing the potential disturbing impact of the fNIRS protocol on the subjects, each experimental
155 session was planned during the baboons' routine health inspection at the Station de Primatologie. As

156 part of the health check, subjects were isolated from their social group and anesthetized with an
157 intramuscular injection of ketamine (5 mg/kg - Ketamine 1000®) and medetomidine (50µg/kg -
158 Domitor®). Then Sevoflurane (Sevotek®) at 3 to 5% and atipamezole (250 µg/kg - Antisedan®) were
159 administered before recordings. Each baboon was placed in ventral decubitus position on the table and
160 the head of the individual was maintained using foam positioners, cushions and Velcro strips to remain
161 straight and to reduce potential motion occurrences. Vital functions were monitored (SpO₂, Respiratory
162 rate, ECG, EtCO₂, T°) and a drip of NaCl was put in place during the entire anaesthesia. Before fNIRS
163 recordings, temporal areas on the baboons' scalp were shaved and sevoflurane inhalation was stopped.
164 Subjects were further sedated with a minimal amount of intravenous injection of Propofol (Propovet®)
165 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
166 the recovery period, subjects were put back in their social group and monitored by the veterinary staff.
167



168
169 **Figure 2:** fNIRS optode and channel locations according to 89 baboons T1 MRI template (Love et al.
170 2016). Blue and green crosses represent optical receivers and transmitters respectively. Ch1, Ch2 and
171 Ch3 indicate the three channels on the right and left temporal cortex.

172 2.3.2. Analysis

173 SPM_fNIRS toolbox (Tak et al. 2016) and custom made codes on Matlab 7.4 R2009b (The MathWorks
174 Inc. 2009) were used to perform first level analysis on raw fNIRS data following this procedure:
175 *i)* O₂Hb concentration changes were calculated using the Beer-Lambert law (Delpy et al. 1988); *ii)*
176 motion artifacts were removed manually in each individual and each channel. In total, 10 seconds
177 (1.3%) were removed from the O₂Hb signal of Rubis and 35 seconds (4.8%) for Talma and Chet; *iii)* a
178 low-pass filter based on the HRF (Friston et al. 2000) was applied to reduce physiological confounds;
179 *iv)* a baseline correction was applied in subtracting the pre-stimulus baseline from the post-stimulus
180 O₂Hb concentration changes of each trial and *v)* O₂Hb signal was averaged for Talma in a window of
181 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
182 onset in order to select the range of maximum O₂Hb concentration changes following Debracque et al
183 2021. Shortly, the differences of concentration range are explained by the presence of tachycardia

184 episodes for both Rubis and Chet during the experiment, involving an HRF almost twice as fast as the
185 one found for Talma.

186 The second level analysis was made on R. studio (Team 2020) using the permuco package (Frossard
187 and Renaud 2019). In each Hemisphere (right, left), we used non-parametric permutation tests with
188 5000 iterations to assess O₂Hb concentration changes for each subject (Talma, Rubis, Chet) as they
189 enable repeated measures ANOVA in small sample sizes by multiplying the design and response
190 variables (Kherad-Pajouh and Renaud 2015). *Stimuli* (call, white noise); *Species* (baboon, chimpanzee);
191 *Channels* (ch1, ch2, ch3) and *Sides* (right, left, both ears) were selected as fixed factors. As
192 recommended, contrast effects of *Species* and *Stimuli* within channels were assessed with 2000
193 permutations (Kherad-Pajouh and Renaud 2015). Both p. values for permutation F (p_{perm}) and
194 parametric F are reported.

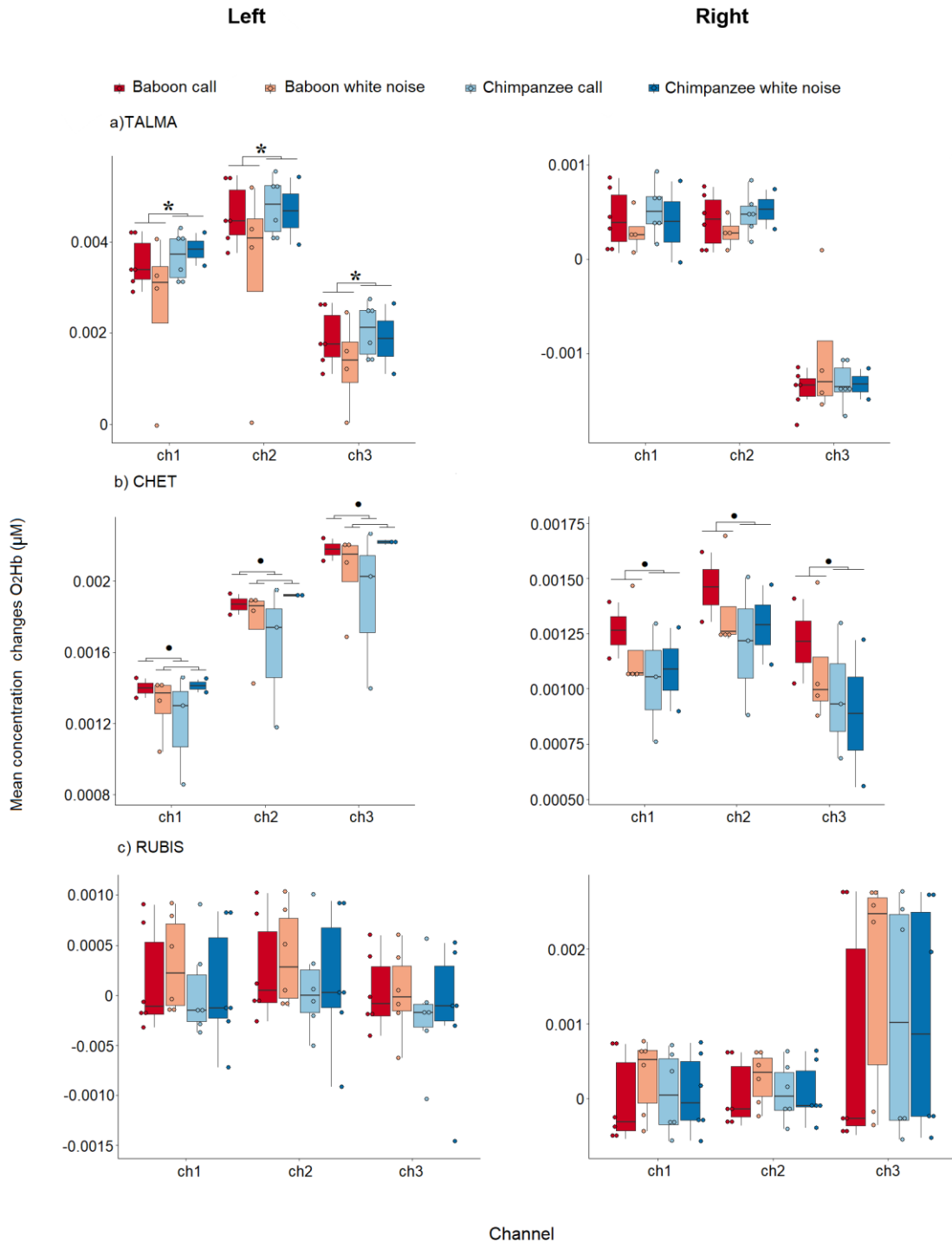
195 3. Results

196 The main effect *Channels* was significant in nearly all subjects and hemispheres: Talma (right: $F(2,3)$
197 = 161,5, $p | p_{\text{perm}} < .001$; left: $F(2,3) = 33.91$, $p | p_{\text{perm}} < .001$); Rubis (right: $F(2,3) = 8,99$, $p | p_{\text{perm}}$
198 $< .001$); and Chet (right: $F(2,3) = 3,99$, $p | p_{\text{perm}} < .05$; left: $F(2,3) = 25.68$, $p | p_{\text{perm}} < .001$). It was not
199 significant for Rubis' left hemisphere ($F(2,3) = 2.15$, $p | p_{\text{perm}} = .12$). Hence, we reported the effects of
200 *Species* and *Stimuli* according to channels in Figure 3. Note that for all subjects, the factor *Sides* did not
201 reach significance and thus, do not statistically explain differences for *Stimuli* and *Species* (see
202 Debracque et al. 2021 for more details related to auditory asymmetries). All results are reported in
203 Supplementary Materials.

204 Regarding the right hemisphere, permutation tests revealed for Chet a significant main effect of the
205 factor *Species* ($F(1,2) = 5.03$, $p | p_{\text{perm}} < .05$).

206 Regarding the left hemisphere, the main factors *Species* was found significant for the baboon Talma
207 ($F(1,2) = 4.24$, $p | p_{\text{perm}} < .05$). In addition, a significant two-way interaction was found significant for
208 the subject Chet between *Stimuli* and *Species* ($F(1,4) = 4,13$, $p | p_{\text{perm}} = .05$).

209 In sum, across the three channels, more O₂Hb concentration changes were found in Talma's left
210 hemisphere for the perception of chimpanzee sounds compared to baboon stimuli. Conversely, for Chet,
211 permutation analyses revealed more O₂Hb concentration changes in the right hemisphere for the passive
212 listening of baboon sounds comparing to chimpanzee ones. Additionally, her left hemisphere was more
213 activated by baboon calls vs. chimpanzee calls and by chimpanzee white noises vs. baboon white noises.



214

215 **Figure 3:** Right and left temporal cortex activations for the baboons **a)** Talma, **b)** Chet and **c)** Rubis
216 during the perception of agonistic baboon (conspecific) and chimpanzee (heterospecific) vocalizations
217 as well as their energy matched white noises. The mean concentration changes of O₂Hb (y axis) is
218 represented in micro molar (µM) for each fNIRS channel (x axis). Colourful dots and dark lines
219 represent stimuli and confidence intervals respectively. Results of the permutation tests within channels
220 are shown with * p<.05; p=.07. The ggplot2 package (Wickham et al. 2021) on R.studio (Team 2020)
221 was used for visualizing the data.

222 4. Discussion

223 The present fNIRS study suggests, in two out of our three tested baboons, a sensitivity of the baboons'
224 temporal cortex for conspecific sounds with documented differential activations in contrast to
225 heterospecific sounds.

226 This finding is quite consistent with the few existing fMRI data in macaques showing the distinctive
227 role of STG in the perception of emotions in conspecific and heterospecific calls (Joly et al. 2012;
228 Petkov et al. 2008). Similar to humans (Belin et al. 2008; Fritz et al. 2018), this first result suggests a
229 different involvement of temporal regions in NHP for the processing of emotions in conspecifics and
230 heterospecific primate vocalizations. From an evolutionary perspective, this would be a mechanism
231 inherited from the common ancestor of *Homo sapiens* and other *Catharrhini* around 40 million years ago
232 (Harrison 2013), although it may be earlier if *Platyrrhini* share this feature too.

233 Despite the significant main effect *Species* for two subjects, fNIRS data revealed also inter-individual
234 differences between Talma and Chet. First, we failed to record significant results for Rubis, although
235 this may have been a consequence of her constant tachycardia during the health check and experiment
236 (see Debracque et al. 2021). Second, the left temporal cortex of Talma was overall more activated for
237 chimpanzee sounds (calls and white noise) than for baboon ones; in contrast, results were reversed in
238 the left temporal cortex of Chet, where statistical analyses highlighted an increase of O₂Hb
239 concentration changes in the left temporal cortex for the passive listening of agonistic baboon sounds
240 compared to chimpanzee sounds. In addition, in her right temporal cortex, we documented an increase
241 in O₂Hb concentration led by the perception of agonistic baboon call.

242 Differences between individuals in temporal cortex sensitivity could explain this absence of congruence
243 in our fNIRS data. Xu and colleagues (2019), have in fact, demonstrated in five anaesthetized and awake
244 macaques great individual variabilities in functional connectivity across cortical regions (Xu et al.
245 2019). Interestingly, the authors compared macaques' fMRI data to human ones and concluded to a
246 similar heterogeneity in functional connectivity across primate species. In the same line, Pernet and
247 colleagues also demonstrated, using fMRI, high inter-individuality differences between human STG
248 and STS for the listening of conspecific emotional voices compared to non-vocal sounds (Pernet et al.
249 2015). Hence, as for highly cited human neuroimaging studies (Szucs and Ioannidis 2020), future non-
250 invasive comparative research should include more subjects to take in consideration this inter-individual
251 variability in brain mechanisms. Yet, the necessity to increase NHP subjects to address limits in
252 statistical power faces ethical aspects related to animal welfare in the case of invasive neuroimaging
253 studies. The development of fNIRS (Debracque et al. 2021) and longitudinal studies in comparative
254 neuroscience (Song et al. 2021) would thus allow answering parts of these challenges.

255 Often explored using fMRI or Pet scan (e.g. Bodin et al. 2021; Gil-da-Costa et al. 2004; Ortiz-Rios et
256 al. 2015), our fNIRS data remain inconclusive regarding any differences in temporal cortex activity

257 between the passive listening of agonistic baboon vocalizations and white noises. Indeed, comparative
258 research on macaques and marmoset (*Callithrix jacchus*) showed a greater sensitivity of the temporal
259 cortex in its anterior part than in its posterior area for the contrast conspecific calls vs. control sounds
260 (Bodin et al. 2021). Future fNIRS studies should improve the probe location on the scalp of baboons or
261 any other NHP species.

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

267 Overall, highlighting the evolutionary continuity between humans and NHP, our results suggest the
268 existence in baboons of differences in temporal cortex activity between the processing of conspecific
269 and heterospecific sounds. Yet, fNIRS data also pointed out high inter-individual variability in these
270 results and remain inconclusive in regards to the contrast conspecific agonistic vocalizations vs. white
271 noises (control sounds), which are often explored meaningfully using fMRI or Pet scan (e.g. Bodin et
272 al. 2021; Gil-da-Costa et al. 2004; Ortiz-Rios et al. 2015). Moreover, the present study has some
273 limitations. Firstly, our experiment focused on baboons and it is unclear whether it will replicate in
274 other monkey species. In fact, Fitch and Braccini (2013) have already suggested differences between
275 monkey in terms of mechanisms for the processing of conspecific and heterospecific vocalizations
276 (Fitch and Braccini 2013). Finally, only agonistic vocalizations were included in the present fNIRS
277 protocol. Yet, similar to humans, NHP might have some distinctive brain mechanisms for negative and
278 positive emotions (e.g. Davidson 1992; Frühholz and Grandjean 2013; Zhang et al. 2018).
279 Consequently, future studies should consider the inclusion of positive emotions, more individuals or
280 the use of fNIRS and longitudinal studies, as well as various monkey species in order to maximize the
281 generalization of their neuroimaging data on auditory processing of emotions in NHP.

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287 **Declarations**

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294 ***Conflict of interest***

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

296 ***Availability of data and material***

297 Raw data are freely available to any researcher.

298 ***Code availability***

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

300 ***Ethics approval***

301 All animal procedures were approved by the “C2EA -71 Ethical Committee of neurosciences” (INT
302 Marseille) under the application number APAFIS#13553-201802151547729, and were conducted at
303 the Station de Primatologie CNRS (UPS 846, Rousset-Sur-Arc, France) within the agreement number
304 C130877 for conducting experiments on vertebrate animals. All methods were performed in accordance
305 with the relevant French law, CNRS guidelines and the European Union regulations (Directive
306 2010/63/EU).

307 ***Consent to participate***

308 Not applicable.

309 ***Consent for publication***

310 Not applicable.

311 **References**

- 312 Bach, Dominik, Didier Grandjean, David Sander, Marcus Herdener, Werner Strik, and Erich Seifritz.
313 2008. “The Effect of Appraisal Level on Processing of Emotional Prosody in Meaningless
314 Speech.” *NeuroImage* 42:919–27. doi: 10.1016/j.neuroimage.2008.05.034.
- 315 Balardin, Joana B., Guilherme A. Zimeo Morais, Rogério A. Furucho, Lucas Trambaiolli, Patricia
316 Vanzella, Claudinei Biazoli, and João R. Sato. 2017. “Imaging Brain Function with
317 Functional Near-Infrared Spectroscopy in Unconstrained Environments.” *Frontiers in Human
318 Neuroscience* 11. doi: 10.3389/fnhum.2017.00258.
- 319 Barreda, Santiago. 2015. *phonTools: Tools for Phonetic and Acoustic Analyses* [computer program].
320 Version 0.2-2.1. <https://CRAN.R-project.org/package=phonTools>.

- 321 Belin, Pascal. 2006. "Voice Processing in Human and Non-Human Primates." *Philosophical*
322 *Transactions of the Royal Society B: Biological Sciences* 361(1476):2091–2107. doi:
323 10.1098/rstb.2006.1933.
- 324 Belin, Pascal, Shirley Fecteau, Ian Charest, Nicholas Nicastro, Marc D. Hauser, and Jorge L. Armony.
325 2008. "Human Cerebral Response to Animal Affective Vocalizations." *Proceedings.*
326 *Biological Sciences* 275(1634):473–81. doi: 10.1098/rspb.2007.1460.
- 327 Boas, David A., Clare E. Elwell, Marco Ferrari, and Gentaro Taga. 2014. "Twenty Years of
328 Functional Near-Infrared Spectroscopy: Introduction for the Special Issue." *NeuroImage*
329 85:1–5. doi: 10.1016/j.neuroimage.2013.11.033.
- 330 Bodin, Clémentine, Régis Trapeau, Bruno Nazarian, Julien Sein, Xavier Degiovanni, Joël Baurberg,
331 Emilie Rapha, Luc Renaud, Bruno L. Giordano, and Pascal Belin. 2021. "Functionally
332 Homologous Representation of Vocalizations in the Auditory Cortex of Humans and
333 Macaques." *Current Biology: CB* 31(21):4839–4844.e4. doi: 10.1016/j.cub.2021.08.043.
- 334 Bryant, Gregory A. 2021. "The Evolution of Human Vocal Emotion." *Emotion Review* 13(1):25–33.
335 doi: 10.1177/1754073920930791.
- 336 Davidson, Richard J. 1992. "Anterior Cerebral Asymmetry and the Nature of Emotion." *Brain and*
337 *Cognition* 20(1):125–51. doi: 10.1016/0278-2626(92)90065-T.
- 338 Debracque, Coralie, Thibaud Gruber, Romain Lacoste, Didier Grandjean, and Adrien Meguerditchian.
339 2021. "Validating the Use of Functional Near-Infrared Spectroscopy in Monkeys: The Case
340 of Brain Activation Lateralization in *Papio Anubis*." *Behavioural Brain Research*
341 403:113133. doi: 10.1016/j.bbr.2021.113133.
- 342 Delpy, D. T., M. Cope, P. van der Zee, S. Arridge, S. Wray, and J. Wyatt. 1988. "Estimation of
343 Optical Pathlength through Tissue from Direct Time of Flight Measurement." *Physics in*
344 *Medicine and Biology* 33(12):1433–42.
- 345 Ferrari, Marco, and Valentina Quaresima. 2012. "A Brief Review on the History of Human
346 Functional Near-Infrared Spectroscopy (FNIRS) Development and Fields of Application."
347 *NeuroImage* 63(2):921–35. doi: 10.1016/j.neuroimage.2012.03.049.
- 348 Fitch, W. Tecumseh, and Stephanie N. Braccini. 2013. "Primate Laterality and the Biology and
349 Evolution of Human Handedness: A Review and Synthesis." *Annals of the New York*
350 *Academy of Sciences* 1288:70–85. doi: 10.1111/nyas.12071.
- 351 Friston, K. J., O. Josephs, E. Zarahn, A. P. Holmes, S. Rouquette, and J. Poline. 2000. "To Smooth or
352 Not to Smooth? Bias and Efficiency in fMRI Time-Series Analysis." *NeuroImage* 12(2):196–
353 208. doi: 10.1006/nimg.2000.0609.
- 354 Fritz, Thomas, Karsten Mueller, Anika Guha, Andre Gouws, Liat Levita, Timothy J. Andrews, and
355 Katie E. Slocombe. 2018. "Human Behavioural Discrimination of Human, Chimpanzee and
356 Macaque Affective Vocalisations Is Reflected by the Neural Response in the Superior
357 Temporal Sulcus." *Neuropsychologia* 111:145–50. doi:
358 10.1016/j.neuropsychologia.2018.01.026.
- 359 Frossard, Jaromil, and Olivier Renaud. 2019. "Permutation Tests for Regression, ANOVA and
360 Comparison of Signals : The Permuco Package." 32.

- 361 Frühholz, Sascha, and Didier Grandjean. 2013. "Multiple Subregions in Superior Temporal Cortex
362 Are Differentially Sensitive to Vocal Expressions: A Quantitative Meta-Analysis."
363 *Neuroscience and Biobehavioral Reviews* 37(1):24–35. doi: 10.1016/j.neubiorev.2012.11.002.
- 364 Fuster, Joaquín, Michael Guiou, Allen Ardestani, Andrew Cannestra, Sameer Sheth, Yong-Di Zhou,
365 Arthur Toga, and Mark Bodner. 2005. "Near-Infrared Spectroscopy (NIRS) in Cognitive
366 Neuroscience of the Primate Brain." *NeuroImage* 26(1):215–20. doi:
367 10.1016/j.neuroimage.2005.01.055.
- 368 George, M. S., T. A. Ketter, P. I. Parekh, B. Horwitz, P. Herscovitch, and R. M. Post. 1995. "Brain
369 Activity during Transient Sadness and Happiness in Healthy Women." *The American Journal*
370 *of Psychiatry* 152(3):341–51. doi: 10.1176/ajp.152.3.341.
- 371 Ghazanfar, Asif A., and Marc D. Hauser. 2001. "The Auditory Behaviour of Primates: A
372 Neuroethological Perspective." *Current Opinion in Neurobiology* 11(6):712–20. doi:
373 10.1016/S0959-4388(01)00274-4.
- 374 Ghazanfar, Asif A., and Laurie R. Santos. 2004. "Primate Brains in the Wild: The Sensory Bases for
375 Social Interactions." *Nature Reviews Neuroscience* 5(8):603–16. doi: 10.1038/nrn1473.
- 376 Gil-da-Costa, Ricardo, Allen Braun, Marco Lopes, Marc D. Hauser, Richard E. Carson, Peter
377 Herscovitch, and Alex Martin. 2004. "Toward an Evolutionary Perspective on Conceptual
378 Representation: Species-Specific Calls Activate Visual and Affective Processing Systems in
379 the Macaque." *Proceedings of the National Academy of Sciences* 101(50):17516–21. doi:
380 10.1073/pnas.0408077101.
- 381 Gil-da-Costa, Ricardo, and Marc D. Hauser. 2006. "Vervet Monkeys and Humans Show Brain
382 Asymmetries for Processing Conspecific Vocalizations, but with Opposite Patterns of
383 Laterality." *Proceedings of the Royal Society B: Biological Sciences* 273(1599):2313–18. doi:
384 10.1098/rspb.2006.3580.
- 385 Grandjean, Didier. 2020. "Brain Networks of Emotional Prosody Processing." *Emotion Review*. doi:
386 10.1177/1754073919898522.
- 387 Grandjean, Didier, David Sander, Gilles Pourtois, Sophie Schwartz, Mohamed L. Seghier, Klaus R.
388 Scherer, and Patrik Vuilleumier. 2005. "The Voices of Wrath: Brain Responses to Angry
389 Prosody in Meaningless Speech." *Nature Neuroscience* 8(2):145–46. doi: 10.1038/nn1392.
- 390 Greenberg, Leslie S. 2002. "Evolutionary Perspectives on Emotion: Making Sense of What We Feel."
391 *Journal of Cognitive Psychotherapy* 16(3):331–47. doi: 10.1891/jcop.16.3.331.52517.
- 392 Harrison, Terry. 2013. "Catarrhine Origins." Pp. 376–96 in *A Companion to Paleoanthropology*. John
393 Wiley & Sons, Ltd.
- 394 Johnstone, Tom, Carien M. van Reekum, Terrence R. Oakes, and Richard J. Davidson. 2006. "The
395 Voice of Emotion: An fMRI Study of Neural Responses to Angry and Happy Vocal
396 Expressions." *Social Cognitive and Affective Neuroscience* 1(3):242–49. doi:
397 10.1093/scan/nsl027.
- 398 Joly, Olivier, Christophe Pallier, Franck Ramus, Daniel Pressnitzer, Wim Vanduffel, and Guy A.
399 Orban. 2012. "Processing of Vocalizations in Humans and Monkeys: A Comparative fMRI
400 Study." *NeuroImage* 62(3):1376–89. doi: 10.1016/j.neuroimage.2012.05.070.

- 401 Kherad-Pajouh, Sara, and Olivier Renaud. 2015. "A General Permutation Approach for Analyzing
402 Repeated Measures ANOVA and Mixed-Model Designs." *Statistical Papers* 56(4):947–67.
403 doi: 10.1007/s00362-014-0617-3.
- 404 Kim, Hak Yeong, Kain Seo, Hong Jin Jeon, Unjoo Lee, and Hyosang Lee. 2017. "Application of
405 Functional Near-Infrared Spectroscopy to the Study of Brain Function in Humans and Animal
406 Models." *Molecules and Cells* 40(8):523–32. doi: 10.14348/molcells.2017.0153.
- 407 Kotz, Sonja A., Christian Kalberlah, Jörg Bahlmann, Angela D. Friederici, and John-D. Haynes. 2013.
408 "Predicting Vocal Emotion Expressions from the Human Brain." *Human Brain Mapping*
409 34(8):1971–81. doi: 10.1002/hbm.22041.
- 410 Lee, Young-A., Valentine Pollet, Akemi Kato, and Yukiori Goto. 2017. "Prefrontal Cortical Activity
411 Associated with Visual Stimulus Categorization in Non-Human Primates Measured with
412 near-Infrared Spectroscopy." *Behavioural Brain Research* 317:327–31. doi:
413 10.1016/j.bbr.2016.09.068.
- 414 Love, Scott A., Damien Marie, Muriel Roth, Romain Lacoste, Bruno Nazarian, Alice Bertello, Olivier
415 Coulon, Jean-Luc Anton, and Adrien Meguerditchian. 2016. "The Average Baboon Brain:
416 MRI Templates and Tissue Probability Maps from 89 Individuals." *NeuroImage* 132:526–33.
417 doi: 10.1016/j.neuroimage.2016.03.018.
- 418 Ortiz-Rios, Michael, Paweł Kuśmierk, Iain DeWitt, Denis Archakov, Frederico A. C. Azevedo,
419 Mikko Sams, Iiro P. Jääskeläinen, Georgios A. Keliris, and Josef P. Rauschecker. 2015.
420 "Functional MRI of the Vocalization-Processing Network in the Macaque Brain." *Frontiers*
421 *in Neuroscience* 9.
- 422 Pan, Yafeng, Guillermo Borragán, and Philippe Peigneux. 2019. "Applications of Functional Near-
423 Infrared Spectroscopy in Fatigue, Sleep Deprivation, and Social Cognition." *Brain*
424 *Topography* 32(6):998–1012. doi: 10.1007/s10548-019-00740-w.
- 425 Perelman, Polina, Warren E. Johnson, Christian Roos, Hector N. Seuánez, Julie E. Horvath, Miguel
426 A. M. Moreira, Bailey Kessing, Joan Pontius, Melody Roelke, Yves Rimpler, Maria Paula C.
427 Schneider, Artur Silva, Stephen J. O'Brien, and Jill Pecon-Slattery. 2011. "A Molecular
428 Phylogeny of Living Primates." *PLOS Genetics* 7(3):e1001342. doi:
429 10.1371/journal.pgen.1001342.
- 430 Pernet, Cyril R., Phil McAleer, Marianne Latinus, Krzysztof J. Gorgolewski, Ian Charest, Patricia E.
431 G. Bestelmeyer, Rebecca H. Watson, David Fleming, Frances Crabbe, Mitchell Valdes-Sosa,
432 and Pascal Belin. 2015. "The Human Voice Areas: Spatial Organization and Inter-Individual
433 Variability in Temporal and Extra-Temporal Cortices." *NeuroImage* 119:164–74. doi:
434 10.1016/j.neuroimage.2015.06.050.
- 435 Petkov, Christopher I., Christoph Kayser, Thomas Steudel, Kevin Whittingstall, Mark Augath, and
436 Nikos K. Logothetis. 2008. "A Voice Region in the Monkey Brain." *Nature Neuroscience*
437 11(3):367–74. doi: 10.1038/nn2043.
- 438 Pihan, Hans, Eckart Altenmüller, and Hermann Ackermann. 1997. "The Cortical Processing of
439 Perceived Emotion: A DC-Potential Study on Affective Speech Prosody." *NeuroReport*
440 8(3):623–27.
- 441 Plichta, M. M., A. B. M. Gerdes, G. W. Alpers, W. Harnisch, S. Brill, M. J. Wieser, and A. J.
442 Fallgatter. 2011. "Auditory Cortex Activation Is Modulated by Emotion: A Functional near-
443 Infrared Spectroscopy (FNIRS) Study." *NeuroImage* 55(3):1200–1207. doi:
444 10.1016/j.neuroimage.2011.01.011.

- 445 Poremba, Amy, Megan Malloy, Richard C. Saunders, Richard E. Carson, Peter Herscovitch, and
446 Mortimer Mishkin. 2004. "Species-Specific Calls Evoke Asymmetric Activity in the
447 Monkey's Temporal Poles." *Nature* 427(6973):448–51. doi: 10.1038/nature02268.
- 448 Scholkmann, Felix, Stefan Kleiser, Andreas Jaakko Metz, Raphael Zimmermann, Juan Mata Pavia,
449 Ursula Wolf, and Martin Wolf. 2014. "A Review on Continuous Wave Functional Near-
450 Infrared Spectroscopy and Imaging Instrumentation and Methodology." *NeuroImage* 85 Pt
451 1:6–27. doi: 10.1016/j.neuroimage.2013.05.004.
- 452 Song, Xiaowei, Pamela García-Saldivar, Nathan Kindred, Yujiang Wang, Hugo Merchant, Adrien
453 Meguerditchian, Yihong Yang, Elliot A. Stein, Charles W. Bradberry, Suliann Ben Hamed,
454 Hank P. Jedema, and Colline Poirier. 2021. "Strengths and Challenges of Longitudinal Non-
455 Human Primate Neuroimaging." *NeuroImage* 236:118009. doi:
456 10.1016/j.neuroimage.2021.118009.
- 457 Szucs, Denes, and John PA. Ioannidis. 2020. "Sample Size Evolution in Neuroimaging Research: An
458 Evaluation of Highly-Cited Studies (1990–2012) and of Latest Practices (2017–2018) in
459 High-Impact Journals." *NeuroImage* 221:117164. doi: 10.1016/j.neuroimage.2020.117164.
- 460 Taglialetela, Jared P., Jamie L. Russell, Jennifer A. Schaeffer, and William D. Hopkins. 2009.
461 "Visualizing Vocal Perception in the Chimpanzee Brain." *Cerebral Cortex (New York, NY)*
462 19(5):1151–57. doi: 10.1093/cercor/bhn157.
- 463 Tak, S., M. Uga, G. Flandin, I. Dan, and W. D. Penny. 2016. "Sensor Space Group Analysis for
464 FNIRS Data." *Journal of Neuroscience Methods* 264:103–12. doi:
465 10.1016/j.jneumeth.2016.03.003.
- 466 Team, R. 2020. *RStudio: Integrated Development for R*. RStudio. Boston MA: RStudio, Inc.
- 467 The MathWorks Inc. 2009. *MATLAB* [computer program]. Version Version 7.9 (R2009b).
- 468 Wakita, Masumi, Masahiro Shibasaki, Takashi Ishizuka, Joerg Schnackenberg, Michiyuki Fujiawara,
469 and Nobuo Masataka. 2010. "Measurement of Neuronal Activity in a Macaque Monkey in
470 Response to Animate Images Using Near-Infrared Spectroscopy." *Frontiers in Behavioral*
471 *Neuroscience* 4:31. doi: 10.3389/fnbeh.2010.00031.
- 472 Wickham, Hadley, Winston Chang, Lionel Henry, Thomas Lin Pedersen, Kohske Takahashi, Claus
473 Wilke, Kara Woo, Hiroaki Yutani, Dewey Dunnington, and RStudio. 2021. *ggplot2: Create*
474 *Elegant Data Visualisations Using the Grammar of Graphics* [computer program]. Version
475 3.3.5. <https://CRAN.R-project.org/package=ggplot2>.
- 476 Wildgruber, Dirk, Thomas Ethofer, Didier Grandjean, and Benjamin Kreifelts. 2009. "A Cerebral
477 Network Model of Speech Prosody Comprehension." *International Journal of Speech-*
478 *Language Pathology* 11(4):277–81. doi: 10.1080/17549500902943043.
- 479 Xu, Ting, Darrick Sturgeon, Julian S. B. Ramirez, Seán Froudish-Walsh, Daniel S. Margulies, Charles
480 E. Schroeder, Damien A. Fair, and Michael P. Milham. 2019. "Interindividual Variability of
481 Functional Connectivity in Awake and Anesthetized Rhesus Macaque Monkeys." *Biological*
482 *Psychiatry. Cognitive Neuroscience and Neuroimaging* 4(6):543–53. doi:
483 10.1016/j.bpsc.2019.02.005.
- 484 Zatorre, R. J., and P. Belin. 2001. "Spectral and Temporal Processing in Human Auditory Cortex."
485 *Cerebral Cortex (New York, N.Y.: 1991)* 11(10):946–53. doi: 10.1093/cercor/11.10.946.

486 Zhang, Dandan, Yu Zhou, and Jiajin Yuan. 2018. "Speech Prosodies of Different Emotional
487 Categories Activate Different Brain Regions in Adult Cortex: An FNIRS Study." *Scientific*
488 *Reports* 8(1):218. doi: 10.1038/s41598-017-18683-2.

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