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1 **Brain activation lateralization in monkeys (*Papio Anubis*) following asymmetric motor**
2 **and auditory stimulations through functional Near Infrared Spectroscopy**

3

4

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22 **Abstract**

23 Hemispheric asymmetries have long been seen as characterizing the human brain; yet, an
24 increasing number of reports suggest the presence of such brain asymmetries in our closest
25 primate relatives. However, most available data in non-human primates have so far been
26 acquired as part of neurostructural approaches such as MRI, while comparative data in humans
27 are often dynamically acquired as part of neurofunctional studies. In the present exploratory
28 study in baboons (*Papio Anubis*), we tested whether brain lateralization could be recorded non-
29 invasively using a functional Near-Infrared Spectroscopy (fNIRS) device in two contexts:
30 motor and auditory passive stimulations. Under light propofol anaesthesia monitoring, three
31 adult female baboons were exposed to a series of (1) left- *versus* right-arm passive movement
32 stimulations; and (2) left- *versus* right-ear *versus* stereo auditory stimulations while recording
33 fNIRS signals in the related brain areas (i.e., motor central sulcus and superior temporal
34 cortices respectively). For the motor condition our results show that left-arm *versus* right-arm
35 stimulations induced typical contralateral difference in hemispheric activation asymmetries in
36 the three subjects for all three channels. For the auditory condition, we also revealed typical
37 human-like patterns of hemispheric asymmetries in one subject for all three channels, namely
38 (1) typical contralateral differences in hemispheric asymmetry between left-ear *versus* right-
39 ear stimulations, and (2) a rightward asymmetry for stereo stimulations. Overall, our findings
40 support the use of fNIRS to investigate brain processing in non-human primates from a
41 functional perspective, opening the way for the development of non-invasive procedures in
42 non-human primate brain research.

43

44 **Keywords**

45 fNIRS, hemispheric lateralization, primate, motor perception, auditory perception

46 Introduction

47

48 Lateralization is often presented as a key characteristic of the human brain, which separates it
49 from other animal brains (1, 2); yet, an increasing number of studies, particularly in non-human
50 primates (from here onward, primates), dispute this claim in a broad array of topics ranging
51 from object manipulation, gestural communication to producing or listening to species-specific
52 vocalizations (3-8). For instance, several primate studies present behavioral evidence of manual
53 lateralization (4, 9), which have been associated with contralateral hemispheric correlates at
54 the neurostructural level (5, 6). Other examples show orofacial asymmetries during vocal
55 production, as evidenced by more pronounced grimaces on the left side of the mouth, which is
56 suggestive of right hemisphere dominance in monkeys and great apes (7, 8), as has been
57 documented in humans (10). In addition, comparative structural neuroimaging has shown that
58 particular areas known to be leftwardly asymmetric in humans, such as the Planum Temporale
59 in the temporal cortex, presented also leftward asymmetry in both monkeys and great apes (11-
60 14), although the bias at the individual level seems more pronounced in humans (15, 16).

61

62 At the neural functional level using functional Magnetic Resonance Imaging (fMRI) or
63 Positron Emission Tomography (PET) scan, most available studies in primates focused on
64 lateralization of perception of synthesized sinusoidal or more complex vocal signals and
65 reported inconsistent results. For instance, in rhesus macaques (*Macaca mulatta*), the
66 processing of species-specific and/or heterospecific calls as well as non-vocal sounds, elicited
67 various patterns of lateralized activations within the Superior Temporal Gyrus (STG) such as
68 in the left lateral parabelt, either toward the right hemisphere or the left depending on the study
69 (17-20). In chimpanzees (*Pan troglodytes*), a similar PET study reported a rightward activation
70 within STG for processing conspecific calls (21). In general, such a variability of direction of
71 hemispheric lateralization for processing calls appears similar to hemispheric lateralization
72 variability described in humans for language processing depending of the type of auditory
73 information and of language functions that are processed (22-24).

74

75 Compared to the leftward bias suggested for language, research investigating emotion
76 perception in primates has strengthened the idea of a right bias in lateralization specific to
77 emotion processing (3). For example, Parr and Hopkins (25) found that right ear temperature
78 increased in captive chimpanzees when they were watching emotional videos, consistent with
79 a greater right hemisphere involvement (25). The rightward hemisphere bias documented in

80 chimpanzees is also found in other primate species such as olive baboons (*Papio anubis*) during
81 natural interactions, as evidenced by studies investigating the perception of visual emotional
82 stimuli (26-29). Yet, while the right hemisphere has understandably received much focused,
83 the left hemisphere is also involved for emotion processing. For example, Schirmer and Kotz
84 have suggested that the left hemisphere is particularly involved in the processing of short
85 segmental information during emotional prosody decoding (24). Whether this functional
86 differentiation, essential for speech perception in humans (30), is also present in non-humans
87 is unclear. Baboons appear in this respect a particularly interesting animal model to study for
88 lateralization, with several recent studies underlying the similarities in manual and brain
89 asymmetries with humans (5, 14, 31). Furthermore, the baboon brain is on average twice as
90 large as the macaque brain (32), which may facilitate the specific investigation of sensory
91 regions. Finally, this species has all the primary cortical structures found in humans (33).

92

93 However, a major drawback in current studies lies in the complexity with which brain
94 asymmetry can be investigated comparatively in primates. Here, we used functional Near-
95 Infrared Spectroscopy (fNIRS) to test whether the blood oxygen level dependent (BOLD)
96 response in baboon brains differed accordingly between the two hemispheres following left-
97 *versus* right-asymmetric auditory and motor stimulations. fNIRS is a non-invasive optical
98 imaging technique that has been developed to investigate brain processes in potentially at-risk
99 populations such as human premature newborns, but which is now widely used with adult
100 human participants. fNIRS is a relatively young imaging technique, with around two decades
101 of use for functional research (34). Considering its portability and its lessened sensitivity to
102 motion artefacts (35) compared to other non-invasive techniques, it might be an excellent
103 methodology to study brain activations in primates under more ecologically relevant testing
104 conditions, for example with a wireless and wearable device. As a first step, the present study
105 tested fNIRS in baboons immobilized under light anesthesia monitoring. In relation with each
106 of the stimulation types, we targeted relevant corresponding brain regions of interest – the
107 motor cortex within the central sulcus and the auditory cortex regions in the temporal lobe
108 respectively - by positioning the two sets of fNIRS channels in both hemispheres (one by
109 hemisphere for a given region). We predicted that, if fNIRS was suitable to record brain signal
110 in baboons, it would reflect contralateral hemispheric asymmetries in signals for each
111 stimulation type within their corresponding brain region of interest, namely the motor cortex,
112 associated with right- *versus* left-arm movements, and the temporal cortex, associated with the
113 right- *versus* left- *versus* stereo ear auditory presentations. Our latter prediction was modulated

114 by the knowledge that auditory regions are less lateralized, with about fifty percent of fibers
115 projecting in the bilateral regions (36, 37), compared to cortical motor regions.

116

117 **Material & Methods**

118

119 *Subjects*

120 We tested three healthy female baboons (Talma, Rubis and Chet, mean age = 14.6 years, SD ±
121 3.5 years). The subjects had normal hearing abilities and did not present a neurological
122 impairment. All animal procedures were approved by the “C2EA -71 Ethical Committee of
123 neurosciences” (INT Marseille) under the application number APAFIS#13553-
124 201802151547729 v4, and were conducted at the Station de Primatologie CNRS (UPS 846,
125 Rousset-Sur-Arc, France) within the agreement number C130877 for conducting experiments
126 on vertebrate animals. All methods were performed in accordance with the relevant French
127 law, CNRS guidelines and the European Union regulations (Directive 2010/63/EU). All
128 monkeys were born in captivity from 1 (F1) or 2 generations (F2), and are housed in social
129 groups at the Station de Primatologie in which they have free access to both outdoor and indoor
130 areas. All enclosures are enriched by wooden and metallic climbing structures as well as
131 substrate on the group to favour foraging behaviours. Water is available ad libitum and monkey
132 pellets, seeds, fresh fruits and vegetables were given every day.

133 *Subject's hand preference in communicative gesture and bi-manual task*

134 The impacts of subject's handedness on cerebral lateralization of language, motor and visual
135 functions are well known in human neuroscience (38). For that purpose, we report here the
136 hand preference of each baboon during visual communicative gesturing (CG - slapping one
137 hand repetitively on the ground in the direction of a conspecific to threaten it) and during a bi-
138 manual tube task (BM - holding a PVC tube with one hand while removing the food inside the
139 tube with the fingers of the other hand). In both contexts, Talma was left-handed (CG: n=27,
140 HI=-0.56, z-score=-2.89; BM: n=31, HI=-0.42, z-score=-2.33) whereas Rubis showed a
141 preference toward the right hand (CG: n=16, HI=0.25, z-score = 1; BM: n=79, HI= 1, z-
142 score=8.88). Conversely, Chet was left-handed in communicative gesture (n=25, HI = -0.44,
143 z-score = -2.2) but right-handed in the bi-manual tube task (n=11, HI = 0.45, z=score = 1.51).

144

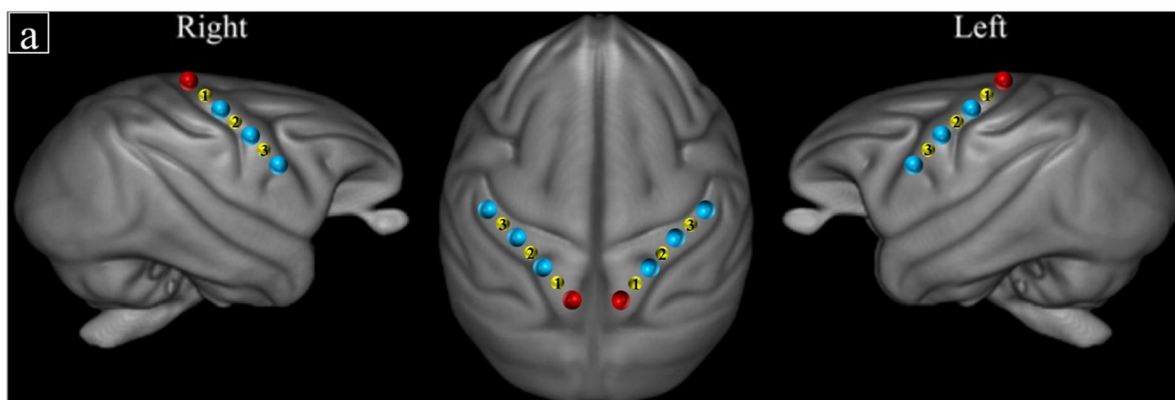
145 *Recordings*

146 We selected one of the most wearable, wireless and light fNIRS devices available on the market
147 (Portalite, Artinis Medical Systems B.V., Elst, The Netherlands) to measure the brain
148 activations in baboons during the motor and auditory stimulations. The data were obtained at
149 50 Hz using six channels (three by hemisphere), three inter-distance probes (3 – 3.5 – 4 cm)
150 and two wavelengths (760 and 850 nm). To localize our regions of interests (ROIs), the motor
151 and auditory cortices, the fNIRS probes were placed using T1 MRI scanner images previously
152 acquired by the LPC group on baboons (see Figure 1).

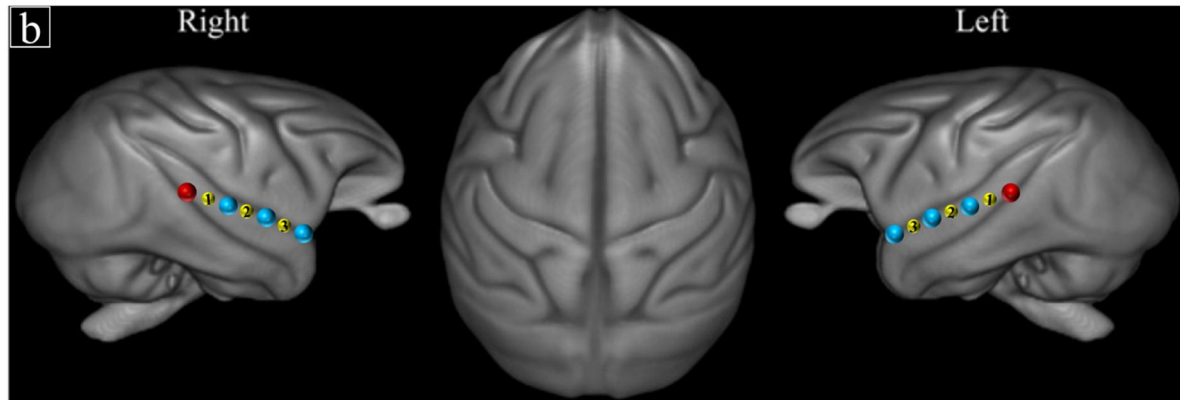
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154 Each fNIRS session was planned during a routine health inspection undergone by the baboons
155 at the Station de Primatologie. As part of the health check, subjects were isolated from their
156 social group and anesthetized with an intramuscular injection of ketamine (5 mg/kg - Ketamine
157 1000®) and medetomidine (50µg/kg - Domitor®). Then Sevoflurane (Sevotek®) at 3 to 5%
158 and atipamezole (250 µg/kg - Antisedan®) were administered before recordings. The area of
159 interest on the scalp was shaved. Each baboon was placed in *ventral decubitus* position on the
160 table and the head of the individual was maintained using foam positioners, cushions and
161 Velcro strips to remain straight and to reduce potential motion occurrences. Vital functions
162 were monitored (SpO₂, Respiratory rate, ECG, EtCO₂, T°) and a drip of NaCl was put in place
163 during the entire anaesthesia. Just before recording brain activations, sevoflurane inhalation
164 was stopped and the focal subject was further sedated with a minimal amount of intravenous
165 injection of Propofol (Propovet®) with a bolus of around 2mg/kg every 10 to 15 minutes or by
166 infusion rate of 0.1 – 0.4 mg/kg/min. After the recovery period, baboons were put back in their
167 social group at the Station de Primatologie and monitored by the veterinary staff.

168



169



170

171 Figure 1: Schematic representation of fNIRS channel locations on ROIs according to T1 MRI
172 template from 89 baboons (39) for (a) the motor and (b) the auditory stimulations. Red and
173 blue dots indicate receivers and transmitters' positions respectively. Yellow dots indicate the
174 channel numbers.

175

176 *Motor stimulations*

177 The motor stimulations consisted of 20 successive extensions of the same arm, alternatively
178 right and left repeated three times according to the same set plan (L-R-R-L-L-R) for all
179 baboons, resulting in a total of 120 arm movements. One experimenter on each side of the
180 baboon extended slowly their respective arm while stimulating the interior side of the hand
181 (gentle rhythmic tapping) with their fingers throughout the duration of the extension (about 5s)
182 upon a brief vocal command triggered by another experimenter. Between each block, there was
183 a 10s lag.

184

185 *Auditory stimulations*

186 The auditory stimuli consisted of 20s-long series of agonistic vocalizations of baboons and of
187 chimpanzees recorded in social settings (in captivity in an outside enclosure for baboons; and
188 in the wild for chimpanzees). Equivalent white noise stimuli matched for the energy dynamics
189 (i.e. the sound envelopes) were produced and used for comparison to control for the sound
190 energy dynamic differences. In the present study and analysis, we only examine the effect of
191 the lateralization of auditory stimulations (i.e., left ear *versus* right ear *versus stereo*) as a whole
192 on hemispheric asymmetry and thus do not distinguish between auditory signal types or species
193 (e.g. white noise and vocalizations). The auditory stimuli were broadcast pseudo-randomly,
194 alternating voiced and white noise stimuli and separated by 15s silences, either binaurally
195 (stereo), only on the left side, or only on the right side. Due to signal artefacts and anaesthesia
196 shortfalls, the number of stimuli between the three baboons differs slightly. For Talma, the total

197 sequence consisted of 37 stimuli; for Rubis, the total sequence consisted of 47 stimuli; and for
198 Chet, the total sequence consisted of 25 stimuli.

199

200 *fNIRS signal*

201 We performed the first level analysis with MatLab 2018b (Mathworks, Natick, MA) using the
202 SPM_fNIRS toolbox (40, https://www.nitrc.org/projects/spm_fnirs/) and homemade scripts.
203 Hemoglobin conversion and temporal preprocessing of O₂Hb and HHb were made using the
204 following procedure:

- 205 1. Hemoglobin concentration changes were calculated with the modified Beer-Lambert
206 law (41);
- 207 2. Motion artifacts were removed manually in each individual and each channel for the
208 auditory stimulations. Thus, 10 seconds in total (1.3%) were removed from the O₂Hb
209 and HHb signals of Rubis and 35 seconds (4.8%) for Talma and Chet fNIRS data;
- 210 3. A low-pass filter based on the hemodynamic response function (HRF) (42) was applied
211 to reduce physiological confounds.
- 212 4. A baseline correction was used for both the motor and auditory stimulations by
213 subtracting respectively (i) the average of 10 seconds intervals preceding each block;
214 (ii) the average of the 15 seconds of silence preceding each sound.

215 According to the temporal properties of the BOLD responses for each baboon, the O₂Hb
216 concentration was averaged for Talma in a window of 4 to 12 s post stimulus onset for each
217 trial; and for Rubis and Chet in a window of 2 to 8 s post stimulus onset in order to select the
218 range of maximum concentration changes (μM). The difference of concentration range is
219 explained by the presence of some tachycardiac episodes for both Rubis and Chet during the
220 experiment, involving an HRF almost twice as fast as the one found for Talma.

221

222 *AQ score calculation*

223 Asymmetry Quotients (AQ) were derived for each subject and each experimental condition
224 (i.e: stimulation of the right arm and of the left arm for the motor experiment; right, left and
225 stereo audio stimulation for the auditory blocks) by first calculating the difference between the
226 right hemisphere (RH) and the left hemisphere (LH) values, to which we subsequently
227 subtracted the same difference during the preceding baseline block for the same subject to
228 normalize across trials. In particular, for motor stimuli, the baseline represented the 10s block
229 without motor activity immediately before a passive stimulation block of the right or left arm.
230 For auditory stimuli, the baseline was calculated on the 15s silence block that immediately

231 preceded the auditory stimuli. In this analysis, all auditory stimuli (baboon and chimpanzee
232 calls, and corresponding white noises) were analysed together. All calculated AQs were then
233 normalized using the scale function of R studio (R studio (2015) Inc., Boston, MA, url:
234 <http://www.rstudio.com/>). For this analysis, we excluded one block ‘chimpanzee white noise
235 audio stereo’ (2.7% of O₂Hb signal) for Rubis, and two blocks ‘chimpanzee white noise audio
236 stereo’ and ‘baboon white noise audio stereo’ (8.3%) for Talma as the recorded data revealed
237 themselves artefactual beyond repair. Positive AQ values indicate a rightward asymmetry and
238 negative values indicate a leftward asymmetry. Finally, using the aov function of R studio, we
239 performed one-way ANOVAs with pairwise comparisons on individual baboons by comparing
240 the AQ of all trials in the different stimulation conditions (right *versus* left motor stimulation;
241 right *versus* left *versus* stereo auditory stimulation) enabling to generalize the data of each
242 individual.

243

244 **Results**

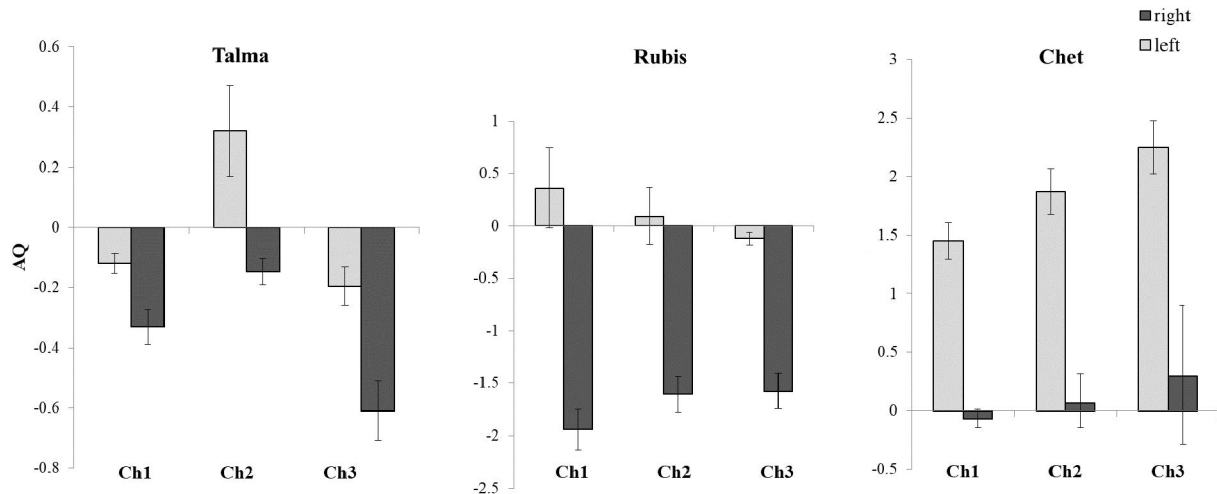
245

246 *Motor stimulations*

247 One-way Anova analyses revealed significant differences between the left and right arm
248 stimulations across the three channels and baboons. Hence, for Rubis and Chet, comparisons
249 between left and right arms stimulations were all significant at $p < .001$ (Rubis: Ch1: $F_{1,118} =$
250 52.63 ; Ch2: $F_{1,118} = 50.63$; and Ch3: $F_{1,118} = 42.35$; for Chet: Ch1: $F_{1,118} = 30.16$; Ch2: $F_{1,118} =$
251 28.21 ; and Ch3: $F_{1,118} = 24.77$). Regarding Talma, significant differences were found at $p < .05$
252 in channel 1 ($F_{1,118} = 3.821$) and channel 3 ($F_{1,118} = 6.521$). The pairwise comparison in channel
253 2 ($F_{1,118} = 14.71$) was significant at $p < .001$.

254 Overall, the difference of AQ between left- *versus* right-arm stimulations were consistently
255 contralateral across the three subjects for all three channels: activation asymmetries were more
256 leftward for right-arm stimulations than for left arm stimulations and, were more rightward for
257 left-arm stimulations than for right arm stimulations (Figure 2; see Table 1 in supplementary
258 material for the mean AQ values).

259



260

261 Figure 2: Normalized averaged AQ (and corresponding SE) in the motor cortex following
262 motor stimulations in the three adult female baboons (see Figure 1 for localization of the
263 channels).

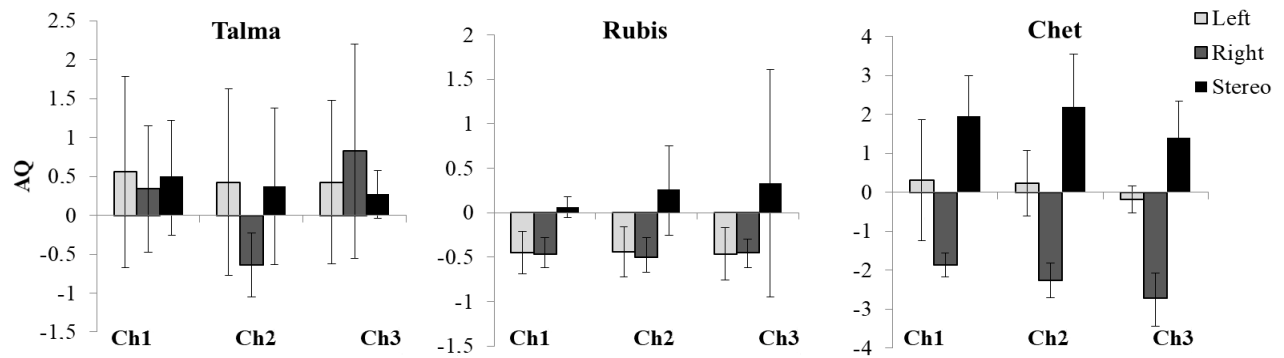
264

265 *Auditory stimulations*

266 We only found significant overall differences between, right, left and stereo ear stimulations
267 ($p < .05$) for subject Chet (Figure 3) for all channels (Ch1: $F_{2,6} = 7.073$; Ch2: $F_{2,6} = 6.473$; and
268 Ch3: $F_{2,6} = 4.289$). Pairwise comparison for right *versus* left ear stimulations were significant
269 ($p < .05$) in Ch1 ($F_{1,6} = 5.216$) and Ch2 ($F_{1,6} = 5.043$). Furthermore, significant differences
270 between right and stereo ear stimulations appeared across all channels (Ch1: $F_{1,6} = 22.55$; Ch2:
271 $F_{1,6} = 16.56$, $p < .001$; Ch3: $F_{1,6} = 15.95$, $p < .05$). Note that the comparison left *versus* stereo did
272 not reach significance for any channels (Ch1: $F_{1,6} = 1.827$; Ch2: $F_{1,6} = 1.825$; Ch3: $F_{1,6} = 0.989$,
273 all $p > .05$).

274 Hence, for Chet, there was a larger bias toward the left hemisphere with right ear stimulation
275 compared to stereo (for all our channels) and left ear stimulation (for channels 1 and 2 only;
276 Figure 3). No difference was recorded as significant for the two other baboons (see Table 2 in
277 supplementary material for the mean AQ values).

278



279

280

281 Figure 3: Normalized averaged AQ (and corresponding SE) above the temporal cortex
282 following auditory stimulations in three adult female baboons (see Figure 1 for localization of
283 the channels).

284

285

286 Discussion

287

288 The results of the present study clearly demonstrate that non-invasive fNIRS is a valid imaging
289 technique to investigate functional lateralization paradigms in a nonhuman primate species.

290

291 Our most potent results were found with the motor stimulation where we observed a strong
292 contralateral hemispheric asymmetry of the fNIRS signals in the motor cortex across baboons.
293 Right arm movements elicited greater leftward asymmetry than left arm movements and *vice*
294 *versa* in each of the three baboons for all three fNIRS channels. Results were clear-cut for
295 Rubis and Chet, though interestingly opposed, with Rubis having a strong leftward asymmetry
296 as a result of her right arm being stimulated, and Chet showing a strong rightward asymmetry
297 for her left arm. Results for Talma were somewhat similar to Rubis' since right arm movements
298 elicited more leftward asymmetry than the left arm in channels 1 and 3. Results in channel 2
299 were most in line with our original prediction, namely a clear mirror pattern of contralateral
300 asymmetries between the two arms: the right arm movements elicited leftward asymmetry and
301 the left arm, a rightward asymmetry. Our results are consistent with previous studies in
302 primates: for arm/hand movements, 90% of the corticospinal pathway project to the
303 contralateral spinal cord (43-47). Hence, our study replicates these findings, with brain signals
304 differences detected by non-invasive fNIRS. Despite the robust consistency of findings across
305 subjects concerning the direction of the effect between the left and the right arms, the reasons
306 for inter-individual variabilities as well as the lack of mirror pattern of results between the two

307 arms (channel 2 of Talma excepted) remains unclear. In particular, potential involuntary
308 differences in arms' stimulation degree between the two experimenters involved in each of the
309 subject's arms manipulations, as well the handedness of each individual baboon may have had
310 an impact on our results.

311

312 Our results were also consistent with predicted asymmetries regarding auditory stimulations
313 for one subject. Contralateral differences of asymmetry were found for Chet in all three
314 channels, with the stimulation of both ears and left ear eliciting overall more rightward
315 asymmetries than right ear stimulations. Nevertheless, for Talma and Rubis, the direction and
316 degree of asymmetry varied irrelevantly of whether the sound was presented to the right or left
317 ear, namely toward the left temporal areas for Rubis and toward the right temporal areas for
318 Talma. These mixed results related to auditory stimulation might be interpreted with respect to
319 some characteristics of the hemispheric organization of the brain. It is well-known that at least
320 one third of the auditory fibres from the olivary complex project to ipsilateral brain regions
321 inducing less lateralization compared to motor brain regions. Furthermore, it has been shown
322 that receptive fields in some regions sensitive to somatosensory input from the auditory cortex
323 are 50% contralateral and 50% bilateral (48, 49); and that temporal regions such as the belt,
324 parabelt and STS receive strong ipsilateral connections in rhesus macaques (50, 51), suggesting
325 overall a less marked lateralization for auditory processing compared to motor regions.
326 Interestingly, the subject's handedness in communicative gesture could also explain these
327 mixed results. In fact, our left-handed subject Talma, showed a clear right hemisphere bias for
328 most stimuli (to the exception of the right ear stimulation in channel 2); whereas Rubis, right-
329 handed in communicative gesture, showed a stronger bias toward the left hemisphere for the
330 sounds broadcast in right and left ears. These preliminary findings may thus highlight the
331 impact of hand preference in communicative contexts on contralateral brain organization in
332 baboons during auditory processing but would need further investigations in a larger cohort of
333 subjects.

334 Overall, given the lack of statistical power related to low sample size, we cannot draw any
335 conclusion regarding the direction of hemispheric lateralizations at a population-level for
336 sounds processing in baboons, or their relation to hand preference for communicative
337 gesturing. Nevertheless, some of our findings remain consistent with the literature on human
338 auditory pathways: for example, Kaiser and collaborators found that stimuli presented in stereo
339 activated more the right hemisphere compared to lateralized sounds showing a left hemisphere
340 bias (52). These results suggest that stereo sounds involve additional processing steps resulting

341 in stronger and more rightward brain activations (53). This pattern of rightward asymmetry for
342 stereo and left sounds processing in the baboon “Chet” is also somewhat consistent with
343 previous rightward asymmetries reported in rhesus monkeys (17) and in chimpanzees (21) for
344 processing conspecific calls. Hence, our data suggest that a phylogenetic functional approach
345 to vocal perception appears possible with fNIRS.

346

347 In conclusion, our study shows that fNIRS is a valid methodology to access brain signals in
348 primates non-invasively. In particular, we have replicated findings in the literature about brain
349 contralateral hemispheric activation in two different modalities showing that fNIRS is able to
350 capture such functional differences even in a context in which baboons were anesthetized.
351 However, we have also uncovered large variation between individuals. This may be due to
352 interindividual differences leading to the inability to precisely record in the same spot for all
353 baboons. Indeed, while we based our placing of optodes on our subjects based on an averaged
354 structural MRI pattern to which all tested individuals contributed, we cannot exclude small
355 variation across cortices. In the future, fNIRS should thus be coupled with structural imaging
356 techniques such as MRI that allow a precise positioning of the optodes for each individual. Yet,
357 the need to couple fNIRS with existing techniques does not deny a more widespread use of
358 fNIRS in the future. To the contrary, we believe that our study opens new avenues for brain
359 investigation in nonhuman primates using fNIRS for two main reasons. First, fNIRS has been
360 used in a multitude of contexts when other brain imaging techniques could not be used, for
361 example in the field with greater ecological conditions (54). While our data have been recorded
362 in anesthetized baboons, a logical next step is to train and habituate baboons to accept wearing
363 a fNIRS device. Our experimental paradigms could then be extended in awake monkeys with
364 more sophisticated design involving behavioural contingencies related to different kinds of
365 stimulation. Second, our study stresses that fNIRS could in the future become a valuable
366 method to explore brain activations in lateral regions in a non-invasive way in nonhuman
367 animals without attempting the physical integrity of the subjects, which would ultimately make
368 investigation of brain mechanisms in animal much more accessible and flexible.

369

370

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380

381

382 References

- 383 1. Eichert N, *et al.* (2019) What is special about the human arcuate fasciculus?
384 Lateralization, projections, and expansion. *Cortex* 118:107-115.
- 385 2. Crow TJ ed (2004) *The speciation of modern Homo sapiens* (Oxford University Press,
386 Oxford).
- 387 3. Lindell AK (2013) Continuities in emotion lateralization in human and non-human
388 primates. *Frontiers in Human Neuroscience* 7:464.
- 389 4. Meguerditchian A, Vauclair J, & Hopkins WD (2013) On the origins of human
390 handedness and language : A comparative review of hand preferences for bimanual
391 coordinated actions and gestural communication in nonhuman primates. *Dev*
392 *Psychobiol* 55:637–650.
- 393 5. Margiotoudi K, *et al.* (2019) Handedness in monkeys reflects hemispheric
394 specialization within the central sulcus. An in vivo MRI study in right- versus left-
395 handed baboons (*Papio anubis*). *Cortex* 118:203-211.
- 396 6. Meguerditchian A, Gardner MJ, Schapiro SJ, & Hopkins WD (2012) The sound of
397 one hand clapping : handedness and perisylvian neural correlates of a communicative
398 gesture in chimpanzees. *Proceeding of the Royal Society Biology* 279:1959-1966.
- 399 7. Fernández-Carriba S, Loeches Á, Morcillo A, & Hopkins WD (2002) Asymmetry in
400 facial expression of emotions by chimpanzees. *Neuropsychologia* 40:1523–1533.
- 401 8. Hook-Costigan MA & Rogers LJ (1998) Lateralized use of the mouth in production
402 of vocalizations by marmosets. *Neuropsychologia* 36:1265–1273.
- 403 9. Fitch WT & Braccini SN (2013) Primate laterality and the biology and evolution of
404 human handedness: A review and synthesis. *Annals of the New York Academy of*
405 *Sciences* 1288:70–85.
- 406 10. Moreno C, Borod J, Welkowitz J, & Alpert M (1990) Lateralization for the expression
407 and perception of facial emotion as a function of age. *Neuropsychologia* 28:199-209.
- 408 11. Hopkins WD, Marino L, Rilling JK, & MacGregor LA (1998) Planum temporale
409 asymmetries in great apes as revealed by magnetic resonance imaging (MRI).
410 *Neuroreport* 9:2913–2918.
- 411 12. Gannon PJ, Holloway RL, Broadfield DC, & Braun AR (1998) Asymmetry of
412 chimpanzee planum temporale: humanlike pattern of Wernicke's brain language area
413 homolog. *Science* 279:220-222.
- 414 13. Pilcher DL, Hammock EAD, & Hopkins WD (2001) Cerebral volumetric
415 asymmetries in non-human primates: A magnetic resonance imaging study. *Laterality*
416 6(2):165-179.
- 417 14. Marie D, *et al.* (2017) Left Brain Asymmetry of the Planum Temporale in a
418 Nonhominid Primate: Redefining the Origin of Brain Specialization for Language.
419 *Cerebral Cortex* 28(5):1808-1815.

- 420 15. Yeni-Komshian GH & Benson DA (1976) Anatomical study of cerebral asymmetry in
421 the temporal lobe of humans, chimpanzees, and rhesus monkeys. *Science* 192:387–
422 389.
- 423 16. Rilling JK (2014) Comparative primate neuroimaging: insights into human brain
424 evolution. *Trends in Cognitive Sciences* 18:46-55.
- 425 17. Poremba A, *et al.* (2004) Species-specific calls evoke asymmetric activity in the
426 monkey's temporal poles. *Nature* 427: 448–451.
- 427 18. Gil-Da-Costa R, *et al.* (2006) Species-specific calls activate homologs of Broca's and
428 Wernicke's areas in the macaque. *Nature Neuroscience* 9(8):1064-1070.
- 429 19. Joly O, Ramus F, Pressnitzer D, Vanduffel W, & Orban GA (2012) Interhemispheric
430 differences in auditory processing revealed by fMRI in awake rhesus monkeys.
431 (Translated from eng) *Cereb Cortex* 22(4):838-853 (in eng).
- 432 20. Petkov CI, *et al.* (2008) A voice region in the monkey brain. *Nature Neuroscience*
433 11:367-374.
- 434 21. Tagliabata JP, Russell JL, Schaeffer JA, & Hopkins WD (2009) Visualizing vocal
435 perception in the chimpanzee brain. *Cerebral Cortex* 19:1151–1157.
- 436 22. Zatorre RJ & Belin P (2001) Spectral and temporal processing in human auditory
437 cortex. *Cerebral Cortex* 11(10):946-953.
- 438 23. Belin P, Zatorre RJ, Lafaille P, Ahad P, & Pike B (2000) Voice-selective areas in
439 human auditory cortex. *Nature* 403(6767):309-312.
- 440 24. Schirmer A & Kotz SA (2006) Beyond the right hemisphere: Brain mechanisms
441 mediating vocal emotional processing. *Trends in Cognitive Sciences* 10:24-30.
- 442 25. Parr LA & Hopkins WD (2000) Brain temperature asymmetries and emotional
443 perception in chimpanzees, Pan troglodytes. *Physiology & Behavior* 71(3-4):363-371.
- 444 26. Casperd JM & Dunbar RIM (1996) Asymmetries in the visual processing of
445 emotional cues during agonistic interactions by gelada baboons. *Behavioural*
446 *Processes* 37(1):57-65.
- 447 27. Morris RD & Hopkins WD (1993) Perception of human chimeric faces by
448 chimpanzees — Evidence for a right-hemisphere advantage. *Brain and Cognition*
449 21(1):111-122.
- 450 28. Baraud I, Buytet B, Bec P, & Blois-Heulin C (2009) Social laterality and
451 'transversality' in two species of mangabeys: Influence of rank and implication for
452 hemispheric specialization. *Behavioural Brain Research* 198(2):449-458.
- 453 29. Wallez C & Vauclair J (2011) Right hemisphere dominance for emotion processing in
454 baboons. *Brain and Cognition* 75(2):164-169.
- 455 30. Grandjean D (2020) Brain Networks of Emotional Prosody Processing. *Emotion*
456 *Review* 0(0):1754073919898522.
- 457 31. Meguerditchian A & Vauclair J (2006) Baboons communicate with their right hand.
458 *Behavioral Brain Research* 171:170-174.
- 459 32. Leigh SR (2004) Brain growth, life history, and cognition in primate and human
460 evolution. *Am J Primatol* 62:139–164.
- 461 33. Kochunov PV, *et al.* (2010) Mapping primary gyrogenesis during fetal development
462 in primate brains: High-resolution in utero structural MRI of fetal brain development
463 in pregnant baboons. *Front Neurosci* 4:1–11.
- 464 34. Boas DA, Elwell CE, Ferrari M, & Taga G (2014) Twenty years of functional near-
465 infrared spectroscopy: Introduction for the special issue. *Neuroimage* 85:1-5.
- 466 35. Ballardin JB, *et al.* (2017) Imaging brain function with Functionnal Near-Infrared
467 Spectroscopy in unconstrained environments. *Front Hum Neurosci* 11:258.

- 468 36. Robinson CJ & Burton H (1980) Organization of somatosensory receptive fields in
469 cortical areas 7b, retroinsula, postauditory and granular insula of *M. fascicularis*. *J*
470 *Comp Neurol* 192(1):69-92.
- 471 37. Smiley JF & Falchier A (2009) Multisensory connections of monkey auditory
472 cerebral cortex. *Hearing Research* 258(1):37-46.
- 473 38. Willems RM, der Haegen LV, Fisher SE, & Francks C (2014) On the other hand:
474 including left-handers in cognitive neuroscience and neurogenetics. *Nature Reviews*
475 *Neuroscience* 15(3):193-201.
- 476 39. Love SA, *et al.* (2016) The average baboon brain: MRI templates and tissue
477 probability maps from 89 individuals. *NeuroImage* 132:526–533.
- 478 40. Tak S, Uga M, Flandin G, Dan I, & Penny WD (2016) Sensor space group analysis
479 for fNIRS data. *Journal of Neuroscience Methods* 264:103–112.
- 480 41. Delpy DT, *et al.* (1988) Estimation of optical pathlength through tissue from direct
481 time of flight measurement. *Phys Med Biol* 33:1433-1442.
- 482 42. Friston KJ, *et al.* (2000) To smooth or not to smooth? Bias and efficiency in fMRI
483 time-series analysis. *NeuroImage* 12(2):196–208.
- 484 43. Dum R. P. & Strick PL (1996) Spinal cord terminations of the medial wall motor
485 Areas in macaque monkeys. *The Journal of Neuroscience* 16:6513–6525.
- 486 44. Brösamle C & Schwab ME (1997) Cells of origin, course, and termination patterns of
487 the ventral, uncrossed component of the mature rat corticospinal tract. *The Journal of*
488 *Comparative Neurology* 386:293–303.
- 489 45. Lacroix S, *et al.* (2004) Bilateral corticospinal projections arise from each motor
490 cortex in the macaque monkey: a quantitative study. *The Journal of Comparative*
491 *Neurology* 473:147–161.
- 492 46. Rosenzweig ES, *et al.* (2009) Extensive spinal decussation and bilateral termination
493 of cervical corticospinal projections in rhesus monkeys. *The Journal of Comparative*
494 *Neurology* 513:151–163.
- 495 47. Heming EA, Cross KP, Takei T, Cook DJ, & Scott SH (2019) Independent
496 representations of ipsilateral and contralateral limbs in primary motor cortex. *eLIFE*.
- 497 48. Robinson CJ & Burton H (1980) Somatotopographic organization in the second
498 somatosensory area of *M. fascicularis*. *J. Comp. Neurol.* 192:43–68.
- 499 49. Smiley J & Falchier A (2009) Multisensory connections of monkey auditory cerebral
500 cortex. *Hearing research* 258.
- 501 50. Cipolloni PB & Pandya DN (1989) Connectional analysis of the ipsilateral and
502 contralateral afferent neurons of the superior temporal region in the rhesus monkey.
503 *The Journal of Comparative Neurology* 281(4):567–585.
- 504 51. Hackett TA, Stepniewska I, & Kaas JH (1998) Subdivisions of auditory cortex and
505 ipsilateral cortical connections of the parabelt auditory cortex in macaque monkeys.
506 *The Journal of Comparative Neurology* 394(4):475–495.
- 507 52. Kaiser J, Lutzenberger W, Preissl H, Ackermann H, & Birbaumer N (2000) Right-
508 Hemisphere Dominance for the Processing of Sound-Source Lateralization. *J.*
509 *Neurosci.* 20(17):6631-6639.
- 510 53. Jäncke L, Wüstenberg T, Schulze K, & Heinze HJ (2002) Asymmetric hemodynamic
511 responses of the human auditory cortex to monaural and binaural stimulation. *Hearing*
512 *Research* 170(1):166–178.
- 513 54. Piper SK, *et al.* (2014) A wearable multi-channel fNIRS system for brain imaging in
514 freely moving subjects. *Neuroimage* 85:64–71.