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3 **On the gestural origins of language :**  
4 **What baboons' gestures and brain have told us after 15 years of research**

5  
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11  
12 Abstract:

13 Nonhuman primates mostly communicate not only with a rich vocal repertoire but also  
14 with manual and body gestures. In contrast to great apes, this latter communicative gestural  
15 system has been poorly investigated in monkeys. In the last 15 years, the gestural research we  
16 conducted in the baboons *Papio anubis*, an Old World monkey species, have shown potential  
17 direct evolutionary continuities with some key properties of language such as intentionality,  
18 referentiality, learning flexibility as well as its underlying lateralization and hemispheric  
19 specialization of the brain. According to these collective findings, which are congruent with  
20 the ones reported in great apes, it is thus not excluded that features of gestural communication  
21 shared between humans, great apes and baboons, may have played a critical role in the  
22 phylogenetic roots of language and dated back, not to the Hominidae evolution, but rather to  
23 their much older Catarrhine common ancestor 25-40 million years ago.

24  
25 KEY WORDS: gestural communication, hemispheric specialization, handedness, primates,  
26 language evolution

27  
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30  
31 Running head: Gestural communication & brain in monkeys

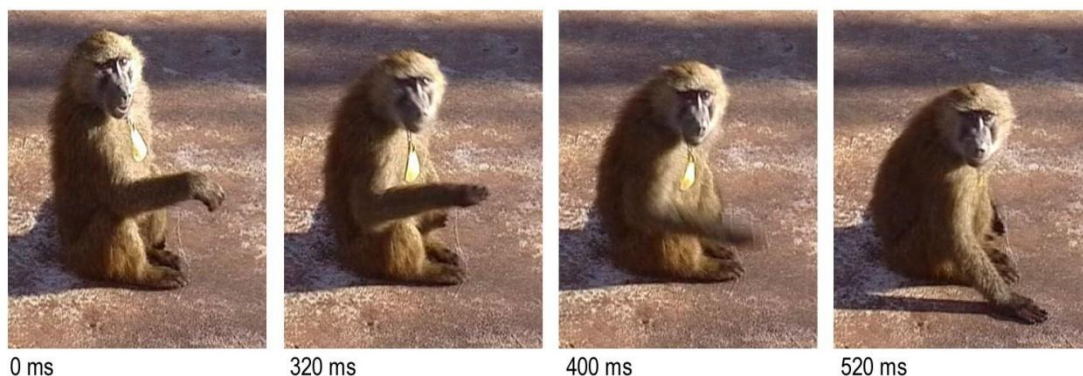
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35 INTRODUCTION

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38 Our research line on gestural communication, just started in the summer 2004 thanks  
39 to a baboon display. I observed a social group of baboons *Papio anubis* at the CNRS  
40 primatology station in South-East of France while I was under the supervision of Pr. Jacques  
41 Vauclair (Meguerditchian & Vauclair, 2006). A young male walked towards me, then stopped  
42 dead. He fixed his gaze on mine and began to repeatedly slam his right hand against the  
43 ground (Figure 1). I remained impassive, but he started again, then changed his strategy: he  
44 opened his mouth, raised his eyebrows when widening his eyes, hit the ground again several  
45 times with one hand, snapped his teeth, shook his head, suddenly stood up, then fell back on his  
46 feet, rubbed forward its both hands on the ground. I took a step forward and here he was  
47 running away, before coming back and repeating his display. In fact, as described initially in  
48 baboons by Kummer (1968), the young baboon sought to intimidate me with this silent parade  
49 of gestures, between play and threat. It turned out that these behaviors seem to meet all the  
50 criteria of what is called "intentional" communication (Leavens 2004). In fact, in absence of

51 the expected response from me, the young baboon seemed to keep trying to reach its  
52 communication goal by repeating his hand slapping gesture and even by changing strategy  
53 and reformulating with other body gestures, much like a teacher varies his explanations to  
54 make himself understood from the audience. In other words, this gestural “persistence”, which  
55 is a typical property of intentional communication described in the development of language  
56 in infants (Bates 1976), might reflect the ability of the baboon to voluntarily produce and  
57 control communication signals (i.e. “hand slap gesture”) to inform the partner (i.e., “me”) of  
58 their goal (i.e., “get away”).

59 In the present paper, before reviewing our research on the gestural system of baboons,  
60 I will start by reminding the need for a large comparative approach across animal species, and  
61 particularly nonhuman primates, on communication and cognition in order to investigate the  
62 multiple phylogenetic roots of language. Then I will review the research we conducted in  
63 baboons on some cognitive aspects of their communicative gestural system, as well as, in a  
64 last part, their manual lateralization and brain hemispheric specialization in comparison with  
65 language organization.

66



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69 Fig. 1. A young male intimidates a human observer by quickly slapping his right-hand on the ground.

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## 72 THE COMPARATIVE APPROACH ON THE ORIGINS OF LANGUAGE

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### 75 *Searching first for the speech origins*

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77  
78 Human language is an extraordinary and unique mean of communication in the animal  
79 kingdom involving complex cognitive functions. To investigate the question of its origins, the  
80 study of the communication systems of our primate cousins, especially the great apes, has  
81 gained unprecedented interest. At the beginning of this quest, the initial scientific debates  
82 focused mostly on the origin of speech-specific features (Boë et al. 2019), such as the  
83 anatomical modification of the vocal apparatus, the larynx and the vocal tract, the articulatory  
84 capacities, the innervation of the tongue, the development of cerebral control for the  
85 production of sounds (e.g., Ploog, 2002) as well as the "syntactic" capacity to generate a  
86 grammar (Chomsky, 1966). However, most of these changes having appeared with the  
87 emergence of *Homo sapiens* approximately 350,000 years ago, the origin of the language was  
88 quite clear: reduced to its verbal and syntactic faculty, language would have emerged as a  
89 single holistic feature with the bifurcation of our species (Chomsky, 1966; Crow, 2002). This

90 turn of the debate thus excluded for a long time the point of view of primatologists on this  
91 question, if it was not to confirm that the apes had indeed neither speech (Hayes, 1952), nor  
92 syntax (Terrace, 1979). Since then, recent studies on monkey vocalizations have challenged  
93 the idea that monkeys cannot speak due to the anatomical constraints of their vocal tract. It  
94 turned out that these constraints, although accurate, are not sufficient to prevent monkeys  
95 from producing vocalizations comparable to human vowels (Boë et al. 2017). The inability to  
96 speak was therefore to be sought elsewhere, likely in the organization of their cognitive and  
97 cerebral systems.

98  
99  
100 *Dislocating the holistic approach on language origins*  
101

102 What if we looked at language other than through its only verbal and syntactic  
103 manifestation? In other words, let's see language, not as an indivisible holistic feature  
104 centered on speech and syntax, but rather as a unique combination of many domain-general  
105 cognitive properties essential to its functioning; a multimodal linguistic system extending to  
106 communicative hand and body gestures as well as facial expressions. Within such a cleverly  
107 orchestrated cognitive assembly, which is unique to human species, are certainly included  
108 generative and grammatical properties but also other fundamental domain-general cognitive  
109 properties such as intentionality, shared attention, learning flexibility, imitation, empathy,  
110 theory of mind, categorization, conceptual mental representation, manipulation of shared  
111 symbolic conventions, referential properties, as well as their underlying hemispheric  
112 specializations of the brain, etc. The list can go on and on (Fitch, 2010).

113 In making such efforts to dislocate the "language" holistic block, it turns out that each  
114 of its cognitive components, taken individually one by one, can potentially be shared with  
115 animals and be evolutionary inherited from a much older common ancestor than *Homo*  
116 *sapiens*. Seeking for the origins of language is therefore not seeking for the origin of this  
117 human "language holistic block" but rather for the origins of each of its many different  
118 cognitive components, thus taking its sources from as many different roots in the history of  
119 evolution. Without "categorization" faculty for instance, it would be difficult for us to speak  
120 given its critical role in the organization of our lexicon. However, this property is not  
121 language-specific and is also useful for organizing our perception of the world. It helps us to  
122 sort the information that we perceive and put it into categories (tools, food, predators ...) to  
123 understand the world, just like most animals such as mice or pigeons (Soto & Wasserman,  
124 2014). This property, which is essential for the organization of language, would thus take root  
125 directly in more general capacities of perceptual categorization, capacities widely shared in  
126 the animal kingdom. In another example, intentional property is characteristic not only of  
127 communication in human language, but also of instrumental actions organized to reach a goal  
128 (e.g., "I'm going to grab this object"), an behavior which is also widely spread in animals (de  
129 Wit & Dickinson 2009). Associative learning is another example of a simple domain-general  
130 property essential to language acquisition: it turned out that even bees are able to learn by  
131 association (e.g., Menzel, 1993)... In evolution of animal cognition, it seems that "nothing is  
132 lost, everything is recycled" and the origins of language certainly benefit from it.

133  
134  
135 *For a large comparative primates approach including monkeys*  
136

137 The question of the origins of language should thus be reformulated as follows: how  
138 these different cognitive properties, which seem to exist in a compartmentalized manner in  
139 certain animals, have, over the course of evolution, started to speak to each other, to work

140 together? How did they end up coordinating to become, in the human species, this unique  
141 constellation of interconnected properties involved specifically in language? In this  
142 framework, the research on the faculties of animals, and of our primate cousins in particular,  
143 has thus become central to investigate the evolution of language and its multiple origins.  
144 These researches should be thus not restricted to humans, nor great apes, but be extended to a  
145 larger comparative approach including monkeys and other animals. For instance, if two  
146 cognitive properties involved in language turn out to work together in the chimpanzee  
147 cognition for example, it is not excluded that this trait may date back to their common  
148 ancestor around 5-9 million years ago. But if this homology extends to an even more  
149 evolutionary distant species, such as the baboon, it may have been inherited from their  
150 common ancestor 25-40 million years ago, and so on. Within such an approach, I will focus  
151 on the research on gestural communicative system in a more distant species, the baboons, and  
152 show how this modality seems to start aggregating, just like in great apes, several key  
153 cognitive features of language.

## 156 157 COGNITIVE PROPERTIES OF GESTURAL COMMUNICATION

### 158 159 160 *Language and gesture*

161  
162 Language involves tight links with communicative gestures. First, we often gesticulate  
163 simultaneously when we speak in signing notably the meaning of our words, such as bringing  
164 closer the index and the thumb in saying “small” (McNeill, 1992). Regarding the interactions  
165 reported between speech and co-speech gestures, it has been suggested that both modalities  
166 might share the same integrated communication system (Gentilucci & Dalla Volta, 2007).  
167 Second, it is well known that intentional communication in infants developed first with the  
168 use of communicative gestures before their first spoken words. Deictic gestures specifically,  
169 such as pointing, seem to play an active role in the development of linguistic abilities (e.g.,  
170 Iverson & Goldin-Meadow, 2005). These collective findings highlight the importance of  
171 gestures in the language system and question their role in language evolution. A growing  
172 number of researchers is supporting the “gestural origins” view that gestural communication  
173 may be the first phylogenetic precursor of human language (e.g., Hewes, 1973; Arbib et al.  
174 2008; Corballis, 2002; Vauclair, 2004), which rely mostly on investigation of the properties of  
175 the gestural communicative system in great apes, particularly chimpanzees primates.

### 176 177 178 *Intentional and referential properties*

179  
180 Interestingly, research in baboons have also reported that, just like in great apes (e.g.  
181 Call & Tomasello, 2007), production of communicative gestures involves a combination of  
182 critical cognitive domain-general properties of language. For instance, some gesture have  
183 been reported to be, not only intentional as mentioned above in the introduction, but also  
184 simultaneously referential, which consist of indicating intentionally external object from the  
185 environment (i.e., food) to a social partner (here a human experimenter). This behavior  
186 requires to orient the attention of the recipient toward this object with imperative pointing  
187 gestures (Meunier et al. 2012). Bourjade et al. (2014) also shown that, when the human social  
188 partner is inattentive, the baboons are able to adjust voluntarily their gestural signals by  
189 producing “noisy” gestures to preliminary get his attention before producing visual pointing

190 gesture. This ability to take into account the attentional state of the recipient when signaling is  
191 typical from intentional and referential communication.

192

193

194 *Flexibility*

195

196 To these two domain-general properties shared with human language, could be also  
197 added and combined the remarkable flexibility of the gestural system in baboons. A recent  
198 ethological study conducted by Molesti et al. (2020) have reported that the gestural repertoire  
199 could reach about 67 visual, tactile, and audible gestures in this species which, just as  
200 chimpanzees or other great apes (Hobaiter et al. 2011; Liebal et al. 2013), not only varied  
201 across individuals and ages but also were used flexibly across different contexts, indicating  
202 means–ends dissociation. This ethological approach also confirms their intentional properties  
203 within intraspecific interactions since baboons produced gestures by looking at the recipient,  
204 then waited for a response and adjusted their gestural signals to the conspecific’s attentional  
205 state (i.e., more visual gestures when the recipient was attending and more tactile gestures  
206 when the recipient was not).

207 Although some of these gestures might be innate (see Byrne et al. 2017), Michael  
208 Tomasello (e.g., Tomasello et al. 1985) explains such a variability by proposing that most of  
209 the gestures in primates would be learned individually through "ontogenetic ritualization" and  
210 that only rare gestures could be socially transmitted through a process of imitation. In other  
211 words, the majority of gestures seems to be the result of an individual process starting initially  
212 from manual actions which would have been gradually ritualized into communicative signals  
213 over the course of the social interactions of the developing individual (Tomasello et al. 1985).  
214 This process constitutes a first major difference from the process of language acquisition, the  
215 vast majority of shared linguistic conventions being rather transmitted by imitation.

216

217

218 *Declarative versus imperative gestures*

219

220 Another major difference is related to the nature of these gestures: these signals in  
221 nonhuman primates do not seem to be “declarative” but rather “imperative”; that is to say that  
222 their gestures are limited, most often, to express a self-centered request to a conspecific such  
223 as "come play with me", "give me this object". In contrast, it seems difficult for them to  
224 referentially communicate to external objects or events for the simple shake of sharing their  
225 attention with others such as "look at this bird" (Tomasello et al. 1985). Given declarative  
226 communication requires, as for learning by imitation, to take into account the mental states of  
227 others (a skill labelled as "theory of mind”), the lack of this communicative skills might be  
228 related to the limitation of their “theory of mind”, an ability which remains controversial in  
229 nonhuman primates. The existence of "imperative" gestures would rather reflect their ability  
230 to learn to associate a gestural response with the goal of the request, via the process of  
231 "ontogenetic ritualization", but not to attribute mental states to others.

232 Nevertheless, the doubt persists since our recent report of a rare and atypical gesture  
233 described in only few baboons, suggesting not only that baboons can flexibly learn new  
234 gestures throughout their life but also that some gestures might be declarative. In fact, we  
235 observed the emergence of a new intentional referential gesture in a female adult baboon,  
236 which consists in searching for mutual gaze with her offspring when rolling between her  
237 fingers a food in front of her baby's face. An atypical behavior we analyzed and interpreted as  
238 a way to draw the attention of the offspring toward this external object without direct  
239 imperative self-centered purpose from the mother. Surprisingly, this behavior seems to fully

240 meet the criteria of joint attention and declarative communication which are both key  
241 properties of language in humans (Meguerditchian et al. 2018; see figure 2).  
242



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244  
245 Fig. 2. An female adult baboon tries to draw the attention of her offspring toward the piece of fruit that  
246 she waves between her fingers. This is the first time that such a “joint attention” gestural behavior has  
247 been observed in this species. © *Laboratoire de Psychologie Cognitive, CNRS, Univ. Aix-Marseille.*  
248

249  
250 Such a combination of domain-general cognitive properties shared between gestural  
251 communication in baboons and language in humans suggest a shared phylogenetical heritage  
252 and continuity between these two communicatory systems. To further investigate such a  
253 hypothesis and exclude any independent evolutionary convergence, it remains critical to  
254 determinate whether the underlying lateralized neural structures of both baboons’ gesture and  
255 human language are also homologue.  
256

## 257 258 259 HEMISPHERIC SPECIALIZATION & GESTURE LATERALIZATION

### 260 261 262 *Hemispheric specialization for language*

263  
264 As many cognitive processes, most language functions involve functional hemispheric  
265 specialization of the brain, which reflects the better aptitude of one hemisphere over the other  
266 for a given function, and/or inter-hemispheric anatomical differences (Josse & Tzourio-  
267 Mazoyer 2004). In a large majority of humans, the left hemisphere is dominant for language  
268 functions such as phonology, semantics or sentence processing (Vigneau et al. 2006) and the  
269 right-hemisphere is dominant for context processing and prosody (Vigneau et al. 2010).  
270 Among such a complex asymmetric neural network, some perisylvian regions play a key-role.  
271 These regions include Broca’s area (Inferior Frontal Gyrus) within the left frontal lobe, as  
272 well as the Superior Temporal Sulcus (STS) in the right temporal lobe and the Planum

273 Temporale in the left temporal lobe. Interestingly, some of these regions for language show  
274 also striking structural inter-hemispheric asymmetry in size (i.e., surface, volume or depth of a  
275 region greater in a hemisphere in comparison to the other). Although their functional  
276 implication remains unclear (e.g., Dorsaint-Pierre et al. 2006; Keller et al. 2011; Tzourio-  
277 Mazoyer et al. 2018), some of these structural asymmetries were initially considered as  
278 anatomical signatures of evolution of the human brain for language and social cognition (e.g.,  
279 Crow, 2002; Leroy et al. 2015).

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### 282 *Handedness is not links with language lateralization*

283

284 This hemispheric specialization for language was initially considered as associated to  
285 handedness. Nearly 90% of humans are right-handed (Annett, 1985). From an evolutionary  
286 view point, there was a strong debate as to whether such population-level right-handedness is  
287 extended to nonhuman primates or is unique and exclusively related to language emergence  
288 and brain specialization for language (Bradshaw & Rogers, 1993; Crow, 2002; Corballis,  
289 2003).

290 This latter view has been challenged by two sets of evidence. First, as many other  
291 studies in terrestrial primates such as humans, chimpanzees and gorillas (Meguerditchian et  
292 al. 2013), we reported that baboons showed population-level right-handedness for bimanual  
293 coordination task, although in a much lower degree than in humans (Vauclair et al. 2005;  
294 Molesti et al. 2016). Interestingly, just like in humans, we also founds that the direction of  
295 handedness was correlated with contralateral depth asymmetry within a section of the central  
296 sulcus, which seems to correspond to the posterior border of the motor hand area  
297 (Margiotoudi et al. 2019). These findings suggest that handedness is not specific to human  
298 evolution and not specific to language emergence. Second, it turned out that direction (left or  
299 right) of handedness in humans is rather a poor marker of the direction of hemispheric  
300 specialization for language, reflecting thus an independent lateralization phenomena (Groen et  
301 al. 2013; Mazoyer et al. 2014; Ocklenburg et al. 2014). This hypothesis find support from  
302 evidence showing that about 70% of left-handed individuals showed also similar left-  
303 hemispheric lateralization for language than right-handed humans (e.g. Knecht et al. 2000).

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### 306 *Lateralization of gestural communication: a better landmark?*

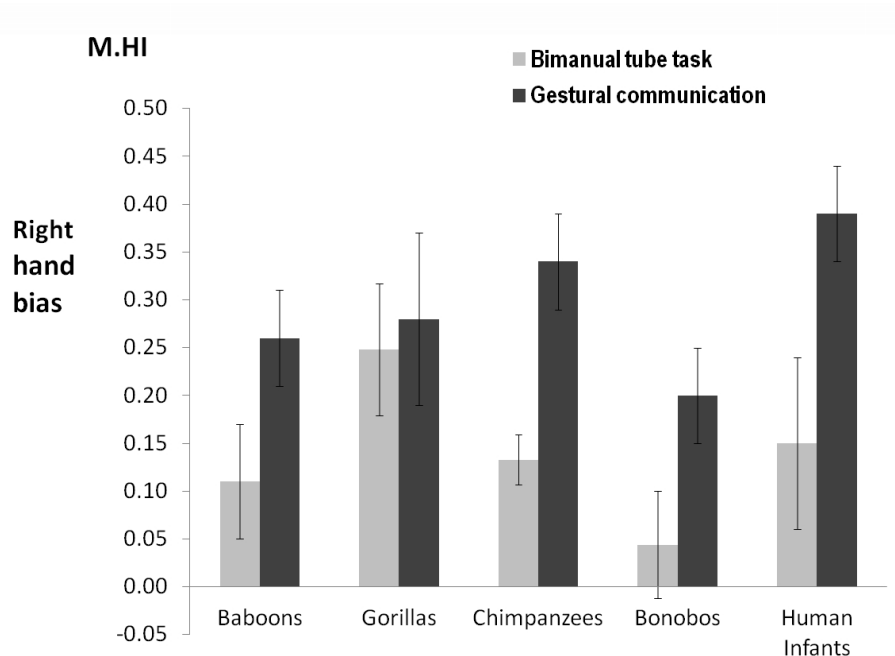
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308 Given its independence from language lateralization, handedness for manipulative  
309 action might be thus not a relevant model to investigate in nonhuman primates its  
310 evolutionary origin. Regarding the strong links reported in the literature between gestural  
311 communication and language in humans (see previous section of the paper) as well as the  
312 language-like combination of domain-general cognitive properties found in the gestural  
313 system of nonhuman primates, manual lateralization for communicative gestures specifically  
314 may constitute a better behavioral candidate.

315 Our research on the lateralization of gestures in baboons provides support to this  
316 hypothesis (Meguerditchian & Vauclair, 2006). As found in children and in chimpanzees  
317 (Meguerditchian et al. 2010, 2013), gestural communication in baboons showed specific  
318 pattern of manual lateralization (see Figure 3). In fact, we found that communicative gestures,  
319 such as the “hand slap” (see Figure 1), elicited not only a more pronounced degree of right-  
320 handedness predominance but also independent individual hand preferences in comparison to  
321 handedness for non-communicative bimanual manipulation (Meguerditchian & Vauclair,  
322 2006, 2009). These findings speak for a greater dominance of the left-hemisphere for



323 communicative gestures which might involve a different lateralized system from the one  
 324 related to handedness for manipulative functions. It is thus not excluded that lateralization of  
 325 communicative gestural system in nonhuman primates might share common prerequisites of  
 326 brain specialization for human language inherited from a common ancestor (Meguerditchian  
 327 et al. 2011).  
 328



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 330  
 331 Fig.3. Degrees of population-level right-handedness (M.H.I: Mean Handedness Index) for species-  
 332 typical communicative gestures in 162 baboons (Meguerditchian et al., 2011), in 18 gorillas, in 70  
 333 chimpanzees (Meguerditchian et al. 2010), in 51 bonobos and whole-hand pointing in 37 human  
 334 infants (see the review of Meguerditchian et al. 2013). Here, the M.H.I are all positive and reflects  
 335 degree of predominance of right-handedness which are more pronounced for gestural communication  
 336 in every species – except in gorillas - compared with the bimanual coordinated task. The error bar  
 337 represents the S.E. around the M.H.I score. *Adapted from Meguerditchian et al. (2013)*  
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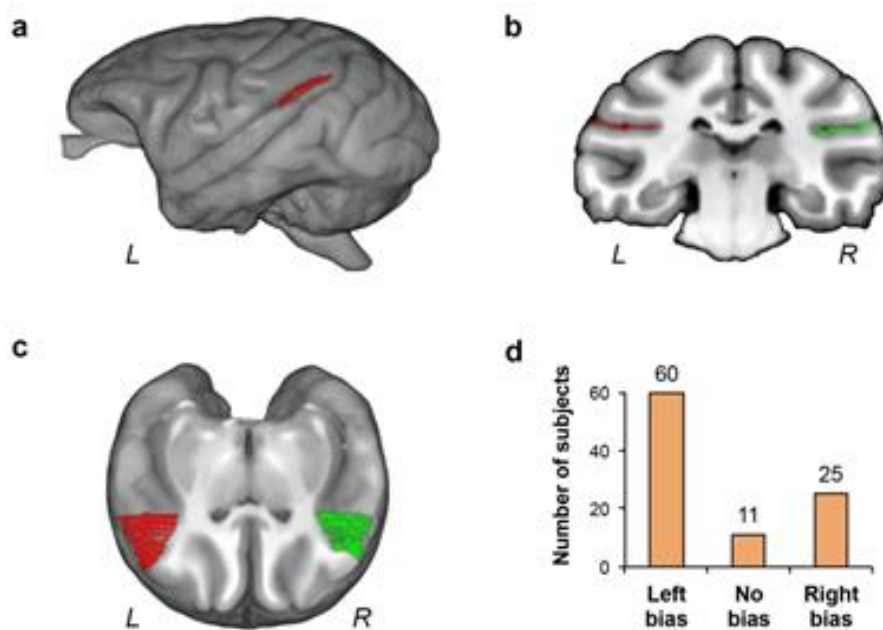
339  
 340 *Brain structural asymmetry in baboons for language homologs*  
 341

342 A key approach to address this latter hypothesis is to investigate in baboons the  
 343 lateralization of brain structures related to language area’s homologs. Most brain studies  
 344 conducted in non-human primates have focused on great apes, particularly chimpanzees, and  
 345 have reported human-like leftward structural asymmetries of a key language region, the  
 346 planum temporale (Gannon et al. 1998; Hopkins et al. 1998). In addition, it was found in  
 347 chimpanzees a contralateral association of asymmetries between (1) inter-hemispheric  
 348 surfaces of the homologs of Broca’s and Wernicke’s areas (Inferior Frontal Gyrus and Planum  
 349 Temporale, respectively) and (2) the direction of manual preferences (i.e. right- *versus* left-  
 350 hand) for communicative gestures (Tagliabue et al. 2006; Hopkins & Nir 2010;  
 351 Meguerditchian et al. 2012).

352 In our cohort of baboons living in social groups, after analyzing 96 anatomical *in vivo*  
 353 cerebral images collected non-invasively using magnetic resonance imaging (MRI), we found  
 354 that a majority of baboons presented a planum temporale’s surface larger in the left  
 355 hemisphere (Marie et al. 2018, see Figure 4) in a quasi-identical distribution to the one

356 originally found in humans (Geschwind & Levitsky 1968). We recently replicate this finding  
 357 in a cohort of 35 newborn baboons, indicating that the leftward planum temporale asymmetry  
 358 is also, just like in prelinguistic infants or in preterm newborn (e.g., Dubois et al. 2010), a  
 359 early feature of the brain organization across development (Becker et al. 2021b, 2021c). In  
 360 addition, according to our on-going studies in those baboons on another sulcus of interest, the  
 361 superior temporal sulcus (STS), a significant human-like neuroanatomical depth asymmetry in  
 362 favor of the right hemisphere was found in a specific portion of this sulcus (Meguerditchian et  
 363 al. 2016), which was initially considered as a human-specific brain lateralization landmark of  
 364 social cognition (Leroy et al. 2015).

365 More importantly, in a recent preprint study focusing on an anatomical marker of the  
 366 Broca area homolog in baboons (i.e., the depth of the ventral portion of the inferior arcuate  
 367 sulcus in the frontal lobe), we found that communicative gesturing's lateralization – but not  
 368 handedness for manipulation - is related to contralateral depth hemispheric asymmetry of this  
 369 marker (Becker et al. 2021a). In other words, baboons communicating with their right hand  
 370 showed a larger Broca area's marker in the left hemisphere and vice et versa. Interestingly, in  
 371 contrast to handedness for object manipulation (see Margiotoudi et al. 2019), gestural  
 372 communication's lateralization is not associated to the central sulcus depth asymmetry,  
 373 suggesting a potential double dissociation of handedness' types between manipulative action  
 374 and gestural communication, as hypothesized in our previous manual lateralization studies.  
 375 This specific lateralized anatomical signature of communicative gesture within the baboons'  
 376 frontal cortex provides thus strong additional support for a phylogenetical gestural  
 377 continuities with language-related frontal hemispheric specialization.  
 378



379  
 380  
 381 Fig. 4. Planum temporale's asymmetry quantification in the baboon brain. A, 3D render of a baboon  
 382 brain and its delineation of the left planum temporale surface area (red). B, Overview of the coronal  
 383 section per coronal section tracing method, one individual coronal section with overlay of left (red)  
 384 and right planum tracing (green). C, Oblique section oriented along both planum temporale of a  
 385 baboon brain (left planum in red, right planum in green) with a clear leftward asymmetry of surface  
 386 area. D, Number of left-biased, non-biased and right-biased baboons for the planum temporale surface  
 387 area according to classification of individual asymmetry quotients (AQ). *Adapted from Marie et al.*  
 388 *(2018)*  
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## CONCLUSION

Our collective research in baboons suggest that combination of cognitive domain-general properties as well as the asymmetric organization of language areas are not specific to human language but extended to far more distant primate species such as the baboon. Interestingly, all those cognitive, behavioral and brain features seems associated with gestural communication in our primate cousins. It is therefore not excluded that some of these prerequisites of language organization may find some phylogenetical roots in gestural communicative system and be inherited, not from Homo Sapiens 350,000 years ago, but rather from the more distant common ancestor of baboons, chimpanzees and humans, 25 to 40 million years ago.

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