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**Review**

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

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

KEY WORDS: gestural communication, hemispheric specialization, handedness, primates, language evolution.

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Running head: Gestural communication and brain in monkeys

INTRODUCTION

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

51 criteria of what is called "intentional" communication (Leavens 2004). In fact, in absence of  
52 the expected response from me, the young baboon seemed to keep trying to reach its  
53 communication goal by repeating his hand slapping gesture and even by changing strategy  
54 and reformulating with other body gestures, much like a teacher varies his explanations to  
55 make himself understood from the audience. In other words, this gestural "persistence", which  
56 is a typical property of intentional communication described in the development of language  
57 in infants (Bates 1976), might reflect the ability of the baboon to voluntarily produce and  
58 control communication signals (i.e. "hand slap gesture") to inform the partner (i.e., "me") of  
59 their goal (i.e., "get away").

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

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## 70 THE COMPARATIVE APPROACH ON THE ORIGINS OF LANGUAGE

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

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75 Human language is an extraordinary and unique mean of communication in the animal  
76 kingdom involving complex cognitive functions. To investigate the question of its origins, the  
77 study of the communication systems of our primate cousins, especially the great apes, has  
78 gained unprecedented interest. At the beginning of this quest, the initial scientific debates  
79 focused mostly on the origin of speech-specific features (Boë et al. 2019), such as the  
80 anatomical modification of the vocal apparatus, the larynx and the vocal tract, the articulatory  
81 capacities, the innervation of the tongue, the development of cerebral control for the  
82 production of sounds (e.g., Ploog 2002) as well as the "syntactic" capacity to generate a  
83 grammar (Chomsky 1966). However, most of these changes having appeared with the  
84 emergence of *Homo sapiens* approximately 350,000 years ago, the origin of the language was  
85 quite clear: reduced to its verbal and syntactic faculty, language would have emerged as a  
86 single holistic feature with the bifurcation of our species (Chomsky 1966; Crow 2002). This  
87 turn of the debate thus excluded for a long time the point of view of primatologists on this  
88 question, if it was not to confirm that the apes had indeed neither speech (Hayes 1952), nor  
89 syntax (Terrace 1979). Since then, recent studies on monkey vocalizations have challenged  
90 the idea that monkeys cannot speak due to the anatomical constraints of their vocal tract. It  
91 turned out that these constraints, although accurate, are not sufficient to prevent monkeys  
92 from producing vocalizations comparable to human vowels (Boë et al. 2017). The inability to  
93 speak was therefore to be sought elsewhere, likely in the organization of their cognitive and  
94 cerebral systems.

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### 97 *Dislocating the holistic approach on language origins*

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99 What if we looked at language other than through its only verbal and syntactic  
100 manifestation? In other words, let's see language, not as an indivisible holistic feature

101 centered on speech and syntax, but rather as a unique combination of many domain-general  
102 cognitive properties essential to its functioning; a multimodal linguistic system extending to  
103 communicative hand and body gestures as well as facial expressions. Within such a cleverly  
104 orchestrated cognitive assembly, which is unique to human species, are certainly included  
105 generative and grammatical properties but also other fundamental domain-general cognitive  
106 properties such as intentionality, shared attention, learning flexibility, imitation, empathy,  
107 theory of mind, categorization, conceptual mental representation, manipulation of shared  
108 symbolic conventions, referential properties, as well as their underlying hemispheric  
109 specializations of the brain, etc. The list can go on and on (Fitch 2010).

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

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132 *For a large comparative primates approach including monkeys*

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

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154 COGNITIVE PROPERTIES OF GESTURAL COMMUNICATION  
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157 *Language and gesture*  
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159 Language involves tight links with communicative gestures. First, we often gesticulate  
160 simultaneously when we speak in signing notably the meaning of our words, such as bringing  
161 closer the index and the thumb in saying “small” (McNeill 1992). Regarding the interactions  
162 reported between speech and co-speech gestures, it has been suggested that both modalities  
163 might share the same integrated communication system (Gentilucci & Dalla Volta 2007).  
164 Second, it is well known that intentional communication in infants developed first with the  
165 use of communicative gestures before their first spoken words. Deictic gestures specifically,  
166 such as pointing, seem to play an active role in the development of linguistic abilities (e.g.,  
167 Iverson & Goldin-Meadow 2005). These collective findings highlight the importance of  
168 gestures in the language system and question their role in language evolution. A growing  
169 number of researchers is supporting the “gestural origins” view that gestural communication  
170 may be the first phylogenetic precursor of human language (e.g., Hewes 1973; Corballis  
171 2003; Vauclair 2004; Arbib et al. 2008), which rely mostly on investigation of the properties  
172 of the gestural communicative system in great apes, particularly chimpanzees primates.  
173

174  
175 *Intentional and referential properties*  
176

177 Interestingly, research in baboons have also reported that, just like in great apes (e.g.  
178 Call & Tomasello 2007), production of communicative gestures involves a combination of  
179 critical cognitive domain-general properties of language. For instance, some gesture have  
180 been reported to be, not only intentional as mentioned above in the introduction, but also  
181 simultaneously referential, which consist of indicating intentionally external object from the  
182 environment (i.e., out of reach food) to a social partner (here a human experimenter). This  
183 behavior requires to orient the attention of the recipient toward this object with imperative  
184 visual pointing gestures (Meunier et al. 2013). In an experimental study conducted in 16 adult  
185 baboons using such a food begging paradigm, Bourjade et al. (2014) proposed to contrast  
186 conditions in which a focal baboon can point to out-of-reach food in front of an experimenter  
187 (1) either facing with eyes open the subject (“attentive partner” condition) or (2) closing her  
188 eyes or showing her back to the subject (“inattentive partner” conditions). This study showed  
189 that, when the human social partner is inattentive, the baboons are able to adjust voluntarily  
190 their gestural signals by increasing their production of “noisy” attention-getting gestures (i.e.,  
191 hand slapping/bagging to the fence) while the visual pointing gestures proportion was higher  
192 in the “attentive partner” condition. This ability to take into account the attentional state of the  
193 recipient when signaling is typical from intentional and referential communication.  
194

195  
196 *Flexibility*  
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198 To these two domain-general properties shared with human language, could be also  
199 added and combined the remarkable flexibility of the gestural system in baboons. A recent  
200 ethological study conducted by Molesti et al. (2020) using continuous focal sampling

201 observations in 47 baboons over 1 year, have reported that the gestural repertoire could reach  
202 about 67 visual, tactile, and audible gestures in this species. After analyzing 2820 focal  
203 sessions (60 sessions of 5 min per subject), this study showed that, just as chimpanzees or  
204 other great apes (Hobaiter & Byrne 2011; Liebal et al. 2013), size of gesture repertoires varied  
205 across individuals and age class (infants, juveniles, subadults and adults) as repertoire size  
206 was found to decrease with age. In addition, after counting the number of different gesture  
207 types used within the same context and the number of contexts in which one gesture type was  
208 used, it turned out that gestures were used flexibly across different contexts indicating means–  
209 ends dissociation. Specifically, while 83.6% of the gesture types of the repertoire were used in  
210 more than one context, several gesture types (i.e., from 16 to 56 gestures) were systematically  
211 recorded for each of the various documented contexts (i.e., affiliative, play, agonistic,  
212 submissive, parental care, sexual, grooming and others). This ethological approach also  
213 confirms their intentional properties within intraspecific interactions since baboons produced  
214 gestures by looking at the recipient, then waited for a response and adjusted their gestural  
215 signals to the conspecific's attentional state (i.e., more visual gestures when the recipient was  
216 attending and more tactile gestures when the recipient was not).

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

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### 228 *Declarative versus imperative gestures*

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230 Another major difference is related to the nature of these gestures: these signals in  
231 nonhuman primates do not seem to be “declarative” but rather “imperative”; that is to say that  
232 their gestures are limited, most often, to express a self-centered request to a conspecific such  
233 as "come play with me", "give me this object". In contrast, it seems difficult for them to  
234 referentially communicate to external objects or events for the simple shake of sharing their  
235 attention with others such as "look at this bird" (Tomasello et al. 1985). According to  
236 Tomasello (2006), given declarative communication requires, as for learning by imitation, to  
237 take into account the mental states of others (a skill labelled as "theory of mind"), the lack of  
238 this communicative skills might be related to the limitation of their “theory of mind”, an  
239 ability which remains controversial in nonhuman primates. The existence of "imperative"  
240 gestures would rather reflect their ability to learn to associate a gestural response with the goal  
241 of the request, via the process of "ontogenetic ritualization", but not to attribute mental states  
242 to others.

243 Nevertheless, such a dichotomy of underlying cognitive processes between imperative  
244 versus declarative communication has been questioned (Leavens & Racine 2009; Leavens  
245 2021). It is indeed not excluded that both type of signals might be both simply reinforced  
246 socially from the partner through the search of social enhancement in both human and apes,  
247 which does not require any high-level social cognitive skills (Leavens et al. 2014; Leavens  
248 2021). In addition, we reported a rare and atypical gesture described in only two female  
249 baboon mothers, suggesting not only that baboons can flexibly learn new gestures throughout  
250 their life but also that some gestures might be also declarative. In fact, we observed the

251 emergence of a new intentional referential gesture in two female adult baboons (Polka and  
252 Fidji), which consists in searching for mutual gaze with her offspring when rolling between  
253 her fingers a food in front of her baby's face (see Fig. 2). An atypical behavior which seems to  
254 fully meet the criteria of joint attention and declarative communication and that we interpreted  
255 as a way to draw the attention of the offspring toward this external object without direct  
256 imperative self-centered purpose from the mother. For both females, those behaviors have  
257 been observed only in the first 6 months of the infant's age when the baby is not able to feed  
258 himself. We also noticed that these behaviors occurred after each birth of a new infant (in four  
259 consecutive birth for Polka and in two consecutive birth for Fidji).

260 Such a combination of domain-general cognitive properties shared between gestural  
261 communication in baboons and language in humans suggest a shared phylogenetical heritage  
262 and continuity between these two communicatory systems. To further investigate such a  
263 hypothesis and exclude any independent evolutionary convergence, it remains critical to  
264 determinate whether the underlying lateralized neural structures of both baboons' gesture and  
265 human language are also homologue.

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## 269 HEMISPHERIC SPECIALIZATION AND GESTURE LATERALIZATION

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### 272 *Hemispheric specialization for language*

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274 As many cognitive processes, most language functions involve functional hemispheric  
275 specialization of the brain, which reflects the better aptitude of one hemisphere over the other  
276 for a given function, and/or inter-hemispheric anatomical differences (Josse & Tzourio-  
277 Mazoyer 2004). In a large majority of humans, the left hemisphere is dominant for language  
278 functions such as phonology, semantics or sentence processing (Vigneau et al. 2006) and the  
279 right-hemisphere is dominant for context processing and prosody (Vigneau et al. 2011).  
280 Among such a complex asymmetric neural network, some perisylvian regions play a key-role.  
281 These regions include Broca's area (Inferior Frontal Gyrus) within the left frontal lobe, as  
282 well as the Superior Temporal Sulcus (STS) in the right temporal lobe and the Planum  
283 Temporale in the left temporal lobe. Interestingly, some of these regions for language show  
284 also striking structural inter-hemispheric asymmetry in size (i.e., surface, volume or depth of a  
285 region greater in a hemisphere in comparison to the other). Although their functional  
286 implication remains unclear (e.g., Dorsaint-Pierre et al. 2006; Keller et al. 2011; Tzourio-  
287 Mazoyer et al. 2018), some of these structural asymmetries were initially considered as  
288 anatomical signatures of evolution of the human brain for language and social cognition (e.g.,  
289 Crow 2002; Leroy et al. 2015).

290

291

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

293

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

299 This latter view has been challenged by two sets of evidence. First, as many other  
300 studies in terrestrial primates such as humans, chimpanzees and gorillas (Meguerditchian et

301 al. 2013), we reported that baboons showed population-level right-handedness for bimanual  
302 coordination task, although in a much lower degree than in humans (Vauclair et al. 2005;  
303 Molesti et al. 2016). Interestingly, just like in humans, we also founds that the direction of  
304 handedness was correlated with contralateral depth asymmetry within a section of the central  
305 sulcus, which seems to correspond to the posterior border of the motor hand area  
306 (Margiotoudi et al. 2019). These findings suggest that handedness is not specific to human  
307 evolution and not specific to language emergence. Second, it turned out that direction (left or  
308 right) of handedness in humans is rather a poor marker of the direction of hemispheric  
309 specialization for language, reflecting thus an independent lateralization phenomena (Groen et  
310 al. 2013; Mazoyer et al. 2014; Ocklenburg et al. 2014). This hypothesis find support from  
311 evidence showing that about 70% of left-handed individuals showed also similar left-  
312 hemispheric lateralization for language than right-handed humans (e.g. Knecht et al. 2000).

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314

315 *Lateralization of gestural communication: a better landmark?*

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

324 Our research on the lateralization of gestures in baboons provides support to this  
325 hypothesis (Meguerditchian & Vauclair 2006). As found in children and in chimpanzees  
326 (Meguerditchian et al. 2010, 2013), gestural communication in baboons showed specific  
327 pattern of manual lateralization (see Fig. 3). In fact, we found that communicative gestures,  
328 such as the “hand slap” (see Fig. 1), elicited not only a more pronounced degree of right-  
329 handedness predominance but also independent individual hand preferences in comparison to  
330 handedness for non-communicative bimanual manipulation (Meguerditchian & Vauclair  
331 2006, 2009). These findings speak for a greater dominance of the left-hemisphere for  
332 communicative gestures which might involve a different lateralized system from the one  
333 related to handedness for manipulative functions. It is thus not excluded that lateralization of  
334 communicative gestural system in nonhuman primates might share common prerequisites of  
335 brain specialization for human language inherited from a common ancestor (Meguerditchian  
336 et al. 2011).

337

338

339 *Brain structural asymmetry in baboons for language homologs*

340

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



351 In our cohort of baboons living in social groups, after analyzing 96 anatomical in vivo  
352 cerebral images collected non-invasively using magnetic resonance imaging (MRI), we found  
353 that a majority of baboons presented a planum temporale's surface larger in the left  
354 hemisphere (Marie et al. 2018, see Fig. 4) in a quasi-identical distribution to the one originally  
355 found in humans (Geschwind & Levitsky 1968). We recently replicate this finding in a cohort  
356 of 35 newborn baboons, indicating that the leftward planum temporale asymmetry is also, just  
357 like in prelinguistic infants or in preterm newborn (e.g., Dubois et al. 2010), an early feature  
358 of the brain organization across development (Becker et al. 2021b, in press). In addition,  
359 according to our on-going studies in those baboons on another sulcus of interest, the superior  
360 temporal sulcus (STS), a significant human-like neuroanatomical depth asymmetry in favor of  
361 the right hemisphere was found in a specific portion of this sulcus (Meguerditchian et al.  
362 2016), which was initially considered as a human-specific brain lateralization landmark of  
363 social cognition (Leroy et al. 2015).

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

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## 380 CONCLUSION

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

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398

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## REFERENCES

409

410

411 Annett MA. 1985. *Left, right, hand and brain: The right shift theory*. Hillsdale (NJ): Erlbaum.

412 Arbib MA, Liebal K, Pika, S. 2008. Primate vocalization, gesture, and the evolution of human  
413 language. *Curr Anthropol.* 49:1053-1063.

414 Bates E. 1976. *Language and context: The acquisition of pragmatics*. New York (NY):  
415 Academic Press.

416 Becker Y, Margiotoudi K, Roth M, Nazarian B, Lacoste R, Anton J-L, Coulon O, Claidière N,  
417 Meguerditchian A. 2021a. On the gestural origin of language lateralization: Manual  
418 communication reflects Broca’s lateralization in monkeys. *bioRxiv*. Preprint.  
419 2021.02.09.430276.

420 Becker Y, Sein J, Velly L, Giacomino L, Renaud L, Lacoste R, Anton J-L, Nazarian B, Berne  
421 C, Meguerditchian A. 2021b. Early left-planum temporale asymmetry in newborn  
422 monkeys (*Papio anubis*): A longitudinal structural MRI study at two stages of  
423 development. *NeuroImage.* 227:117575.

424 Becker Y, Sein J, Velly L, Renaud L, Lacoste R, Meguerditchian A. In press. Planum  
425 temporale grey matter volume asymmetries in new-born monkeys (*Papio anubis*). *Brain*  
426 *Struct Funct*

427 Bradshaw JL, Rogers L. 1993. *The evolution of lateral asymmetries, language, tool-use and*  
428 *intellect*. San Diego (CA): Academic Press.

429 Boë L-J, Berthommier F, Legou T, Captier G, Kemp C, Sawallis TR, Becker Y, Rey A, Fagot  
430 J. 2017. Evidence of a vocalic proto-system in the baboon (*Papio papio*) suggests pre-  
431 hominin speech precursors. *PLoS ONE.* 12(1):e0169321.

432 Boë L-J, Sawallis TR, Fagot J, Badin P, Barbier G, Captier G, Ménard L, Heim, J-L,  
433 Schwartz, J-L. 2019. Which way to the dawn of speech?: Reanalyzing half a century of  
434 debates and data in light of speech science. *Sci Adv.* 5(12):eaaw3916.

435 Bourjade M, Meguerditchian A, Maille A, Gaunet F, Vauclair J. 2014. Olive baboons (*Papio*  
436 *anubis*) adjust their visual and auditory intentional gestures to the visual attention of  
437 others. *Anim Behav.* 87:121-128.

438 Byrne RW, Cartmill E, Genty E, Graham KE, Hobaiter C, Tanner J. 2017. Great ape gestures:  
439 intentional communication with a rich set of innate signals. *Anim Cogn.* 20:755–769.

440 Call J, Tomasello M. 2007. *The gestural communication of apes and monkeys*. New York  
441 (NY): LEA.

442 Chomsky N. 1966. *Cartesian linguistics*. New York (NY): Harper & Row.

443 Corballis MC. 2003. From mouth to hand: Gesture, speech, and the evolution of right-  
444 handedness. *Behav Brain Sci.* 26:199-208.

445 Crow T. 2002. *The speciation of modern Homo sapiens*. Oxford (UK): Oxford University  
446 Press.

447 de Wit S, Dickinson A. 2009. Associative theories of goal-directed behaviour: a case for  
448 animal–human translational models. *Psychol Res.* 73:463–476.

449 Dorsaint-Pierre R, Penhune VB, Watkins KE, Neelin P, Lerch JP, Bouffard M, Zatorre RJ.  
450 2006. Asymmetries of the planum temporale and Heschl's gyrus: relationship to  
451 language lateralization. *Brain*. 129:1164-1176.

452 Dubois J, Benders M, Lazeyras F, Borradori-Tolsa C, Ha-Vinh Leuchter R, Mangin JF, Hüppi  
453 PS. 2010. Structural asymmetries of perisylvian regions in the preterm newborn.  
454 *NeuroImage*. 52:32–42.

455 Fitch WT. 2010. *The evolution of language*. Cambridge (UK): Cambridge University Press.

456 Gannon PJ, Holloway RL, Broadfield DC, Braun AR. 1998. Asymmetry of chimpanzee  
457 planum temporale: Human like pattern of Wernicke's brain language area homolog. *Sci*.  
458 279:220–222.

459 Gentilucci M, Dalla Volta R. 2007. The motor system and the relationships between speech and  
460 gesture. *Gesture*. 7:159-177.

461 Geschwind N, Levitsky W. 1968. Human brain: Left-right asymmetries in temporal speech  
462 region. *Sci*. 161:186–187.

463 Groen MA, Whitehouse AJ, Badcock NA, Bishop DV. 2013. Associations between  
464 handedness and cerebral lateralisation for language: a comparison of three measures in  
465 children. *PLoS ONE*. 8:e64876.

466 Hayes C. 1952. *The ape in our house*. London (UK): Gollancz.

467 Hewes GW. 1973. Primate communication and the gestural origin of language. *Curr*  
468 *Anthropol*. 14:5-24.

469 Hobaiter C, Byrne RW. 2011. The gestural repertoire of the wild chimpanzee. *Anim Cogn*.  
470 14(5):745-767.

471 Hopkins WD, Marino L, Rilling JK, MacGregor LA. 1998. Planum temporale asymmetries in  
472 great apes as revealed by magnetic resonance imaging (MRI). *Neuroreport*. 9:2913-  
473 2918.

474 Hopkins WD, Nir T. 2010. Planum temporale surface area and grey matter asymmetries in  
475 chimpanzees (*Pan troglodytes*): The effect of handedness and comparison within  
476 findings in humans. *Behav Brain Res*. 208:436-443.

477 Iverson JM, Goldin-Meadow S. 2005. Gesture paves the way for language development.  
478 *Psychol Sci*. 16:367-371.

479 Josse G, Tzourio-Mazoyer N. 2004. Hemispheric specialization for language. *Brain Res Rev*.  
480 44(1):1-12.

481 Keller SS, Roberts N, García-Fiñana M, Mohammadi S, Ringelstein EB, Knecht S, Deppe M.  
482 2011. Can the language-dominant hemisphere be predicted by brain anatomy? *J Cogn*  
483 *Neurosci*. 23:2013–2029.

484 Knecht S, Dräger B, Deppe M, Bobe L, Lohmann H, Flöel A, Ringelstein EB, Henningsen H.  
485 2000. Handedness and hemispheric language dominance in healthy humans. *Brain*.  
486 123:2512–2518.

487 Kummer H. 1968. *Social organization of hamadryas baboons*. Chicago (IL): University of  
488 Chicago Press.

489 Leavens DA. 2004. Manual deixis in apes and humans. *Interaction Studies. Social Behaviour*  
490 *and Communication in Biological and Artificial Systems*. 5:387-408.

491 Leavens DA. 2021. The Referential Problem Space revisited: An ecological hypothesis of the  
492 evolutionary and developmental origins of pointing. *Cogn Sci*. a1554:1-21.

493 Leavens DA, Racine TP. 2009. Joint attention in apes and humans: are humans unique? *J*  
494 *Conscious Stud*. 16:240–267.

495 Leavens DA, Sansone J, Burfield A, Lightfoot S, O'Hara S, Todd BK. 2014. Putting the 'joy'  
496 in joint attention: affective-gestural synchrony by parents who point for their babies.  
497 *Front Psychol*. 5(879):1-14.

498 Leroy F, Cai Q, Bogart SL, Dubois J, Coulon O, Monzalvo K, Fischer C, Glasel H, Van der  
499 Haegen L, Bénézit A, et al. 2015. New human-specific brain landmark: The depth  
500 asymmetry of superior temporal sulcus. *PNAS*. 112:1208-1213.

501 Liebal K, Waller BM, Burrows AM, Slocombe KE. 2013. Primate communication: A  
502 multimodal approach. Cambridge (UK): Cambridge University Press.

503 Margiotoudi K, Marie D, Claidière N, Coulon O, Roth M, Nazarian B, Lacoste R, Hopkins  
504 WD, Molesti S, Fresnais P, et al. 2019. Handedness in monkeys reflects hemispheric  
505 specialization within the central sulcus. An in vivo MRI study in right- and left-handed  
506 baboons. *Cortex*. 118:203-211.

507 Marie D, Roth M, Lacoste R, Nazarian B, Bertello A, Anton J-L, Hopkins WD, Margiotoudi  
508 K, Love AS, Meguerditchian A. 2018. Left brain asymmetry of the planum temporale in  
509 a non-hominid primate: Redefining the origin of brain specialization for language.  
510 *Cereb Cortex*. 28, 1808-1815.

511 Mazoyer B, Zago L, Jobard G, Crivello F, Joliot M, Perchey G, Mellet E, Petit L, Tzourio-  
512 Mazoyer N. 2014. Gaussian mixture modeling of hemispheric lateralization for  
513 language in a large sample of healthy individuals balanced for handedness. *PLoS ONE*.  
514 9:e101165.

515 McNeill D. 1992. Hand and mind. Chicago (IL): University of Chicago Press.

516 Meguerditchian A, Gardner MJ, Schapiro SJ, Hopkins WD. 2012. The sound of one hand  
517 clapping: handedness and perisylvian neural correlates of a communicative gesture in  
518 chimpanzees. *Proc R Soc Lond B*. 279:1959-1966.

519 Meguerditchian A, Marie D, Love SA, Margiotoudi K, Bertello A, Lacoste R, Roth M,  
520 Nazarian B, Anton J-L, Coulon O. 2016. Human-like brain specialization in baboons: an  
521 in vivo anatomical MRI study of language areas homologs in 96 subjects. In: Roberts SG, et  
522 al., editors. *The evolution of language. Proceedings of the 11th International Conference*  
523 *(EVOLANG11)*. New Orleans (LA). doi:10.17617/2.2248195.

524 Meguerditchian A, Molesti S, Vauclair J. 2011. Right-handedness predominance in 162  
525 baboons for gestural communication: Consistency across time and groups. *Behav*  
526 *Neurosci*. 125:653-660.

527 Meguerditchian A, Vauclair J. 2006. Baboons communicate with their right hand. *Behav*  
528 *Brain Res*. 171:170-174.

529 Meguerditchian A, Vauclair J. 2009. Contrast of hand preferences between communicative  
530 gestures and non communicative actions in baboons: implications for the origins of  
531 hemispheric specialization for language. *Brain Lang*. 108:167–174.

532 Meguerditchian A, Vauclair J, Hopkins WD. 2010. Captive chimpanzees use their right hand  
533 to communicate with each other: Implications for the origin of the cerebral substrate for  
534 language. *Cortex*. 46:40-48.

535 Meguerditchian A, Vauclair J, Hopkins WD. 2013. On the origins of human handedness and  
536 language: A comparative review of hand preferences for bimanual coordinated actions  
537 and gestural communication in nonhuman primates. *Dev Psychobiol*. 55:637–650.

538 Menzel R. 1993. Associative learning in honey bees. *Apidologie*. 24(3):157-168.

539 Meunier H, Prieur J, Vauclair J. 2013. Olive baboons communicate intentionally by pointing.  
540 *Anim Cogn*. 16:155–163.

541 Molesti S, Meguerditchian A, Bourjade M. 2020. Gestural communication in olive baboons  
542 (*Papio anubis*): repertoire and intentionality. *Anim Cogn*. 23:19–40.

543 Molesti S, Vauclair J, Meguerditchian A. 2016. Hand preferences for unimanual and  
544 bimanual coordinated actions in olive baboons (*Papio anubis*) : consistency over time  
545 and across populations. *J Comp Psychol*. 130:341-350.

546 Ocklenburg S, Beste C, Arning L, Peterburs J, Güntürkün O. 2014. The ontogenesis of  
547 language lateralization and its relation to handedness. *Neuroscience Biobehavioral*  
548 *Reviews*. 43:191-198.

549 Ploog D. 2002. The neural basis of vocalization. In: Crow TJ, editor. *The speciation of*  
550 *modern Homo sapiens*. Oxford (UK): Oxford University Press; p. 121–135.

551 Soto FA, Wasserman EA. 2014. Mechanisms of object recognition: what we have learned  
552 from pigeons. *Front Neural Circuits*. 8:122.

553 Tagliatela JP, Cantalupo C, Hopkins WD. 2006. Gesture handedness predicts asymmetry in  
554 the chimpanzee inferior frontal gyrus. *NeuroReport*. 17:923-927.

555 Terrace HS. 1979. *Nim*. New York (NY): Knopf.

556 Tomasello M. 2006. Why don't apes point? In: Enfield N, Levinson S, editors. *The roots of*  
557 *human sociality: Culture, cognition, and interaction*. Oxford (UK): Berg; p. 506-524.

558 Tomasello M, George B, Kruger A, Farrar M, Evans A. 1985. The development of gestural  
559 communication in young chimpanzees. *J Hum Evol*. 14:175-186.

560 Tzourio-Mazoyer N, Crivello F, Mazoyer B. 2018. Is the planum temporale surface area a  
561 marker of hemispheric or regional language lateralization? *Brain Struct Funct*.  
562 223:1217–1228.

563 Vaclair J. 2004. Lateralization of communicative signals in nonhuman primates and the  
564 hypothesis of the gestural origin of language. *Interaction Studies. Social Behaviour and*  
565 *Communication in Biological and Artificial Systems*. 5:363-384.

566 Vaclair J, Meguerditchian A, Hopkins, WD. 2005. Hand preferences for unimanual and  
567 coordinated bimanual tasks in baboons (*Papio anubis*). *Cogn Brain Res*. 25:210-216.

568 Vigneau M, Beaucousin V, Hervé P-Y, Duffau H, Crivello F, Houdé O, Mazoyer B, Tzourio-  
569 Mazoyer N. 2006. Meta-analysing left hemisphere language areas: phonology,  
570 semantics, and sentence processing. *NeuroImage*. 30:1414-1432.

571 Vigneau M, Beaucousin V, Hervé P-Y, Jobard G, Petit L, Crivello F, Mellet E, Zago L,  
572 Mazoyer B, Tzourio-Mazoyer N. 2011. What is right-hemisphere contribution to  
573 phonological, lexico-semantic, and sentence processing? Insights from a meta-analysis.  
574 *NeuroImage*. 54:577-593.

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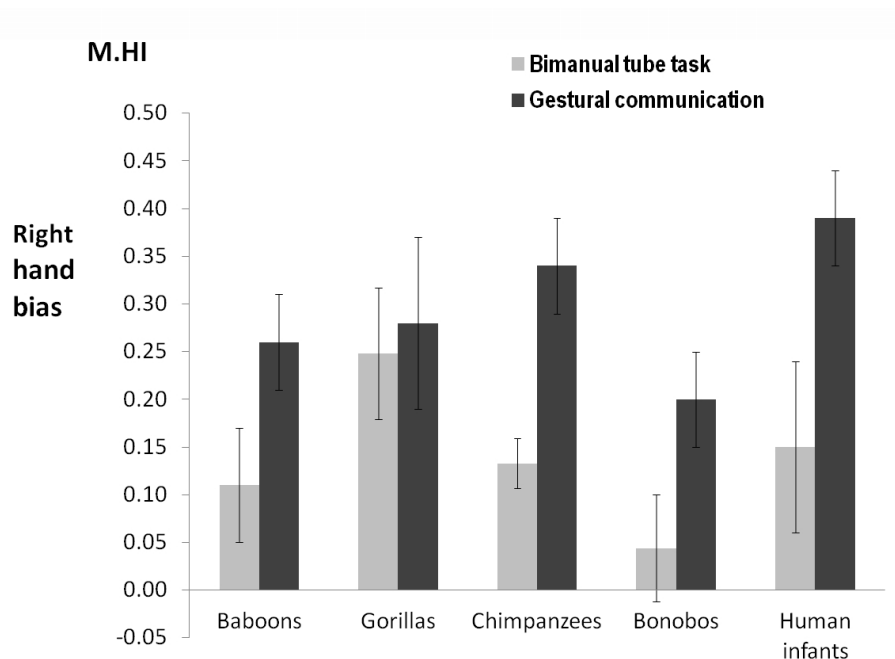


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578 Fig. 1. — A young male intimidates a human observer by quickly slapping his right-hand on the  
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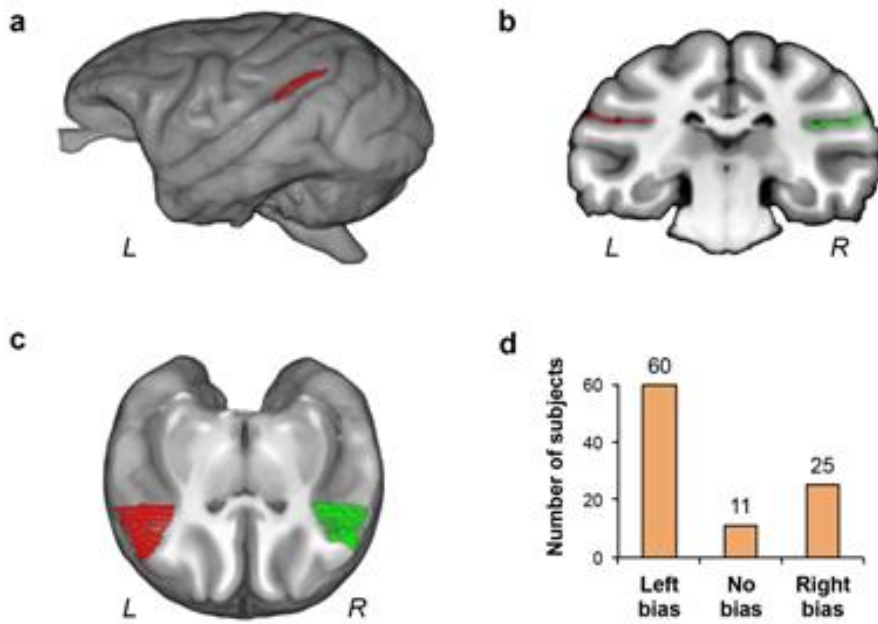
Fig. 2. — An female adult baboon tries to draw the attention of her offspring toward the piece of fruit that she waves between her fingers. This is the first time that such a “joint attention” gestural behavior has been observed in this species. ©Laboratoire de Psychologie Cognitive, CNRS, Univ. Aix-Marseille.



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Fig. 3. — Degrees of population-level right-handedness (M.HI: Mean Handedness Index) for species-typical communicative gestures in 162 baboons (Meguerditchian et al. 2011), in 18 gorillas, in 70 chimpanzees (Meguerditchian et al. 2010), in 51 bonobos and whole-hand pointing in 37 human infants (see the review of Meguerditchian et al. 2013). Here, the M.HI are all positive and reflects degree of predominance of right-handedness which are more pronounced for gestural communication in every species – except in gorillas – compared with the bimanual coordinated task. The error bar represents the SE around the M.HI score. Adapted from Meguerditchian et al. (2013).

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Fig. 4. — Planum temporale's asymmetry quantification in the baboon brain. (a) 3D render of a baboon brain and its delineation of the left planum temporale surface area (red). (b) Overview of the coronal section per coronal section tracing method, one individual coronal section with overlay of left (red) and right planum tracing (green). (c) Oblique section oriented along both planum temporale of a baboon brain (left planum in red, right planum in green) with a clear leftward asymmetry of surface area. (d) Number of left-biased, non-biased and right-biased baboons for the planum temporale surface area according to classification of individual asymmetry quotients (AQ). Adapted from Marie et al. (2018).