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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.
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175 *Intentional and referential properties*
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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.
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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).

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292 *Handedness is not links with language lateralization*

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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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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).

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338

339 *Brain structural asymmetry in baboons for language homologs*

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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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381 CONCLUSION

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

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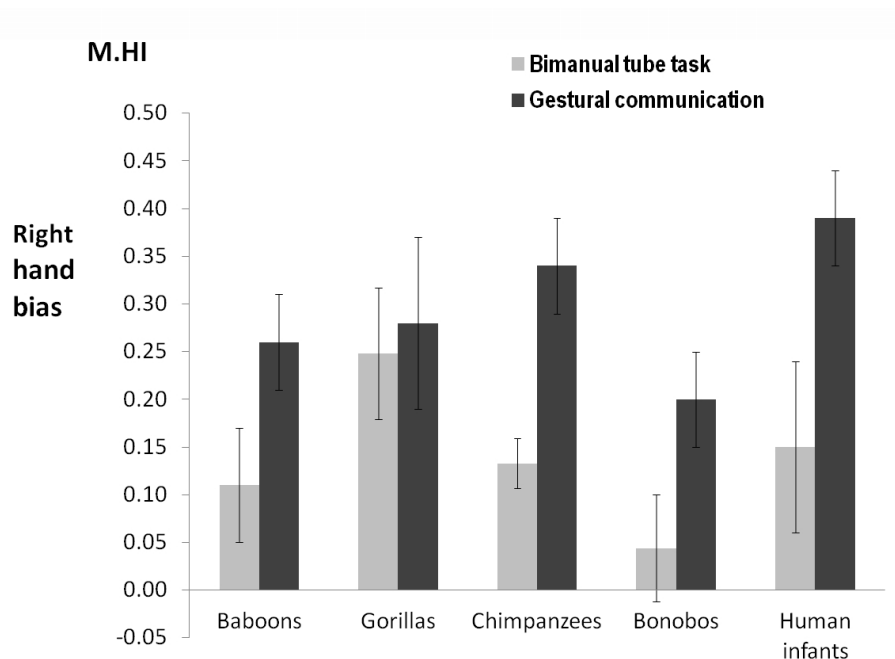


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578 Fig. 1. — A young male intimidates a human observer by quickly slapping his right-hand on the
579 ground.
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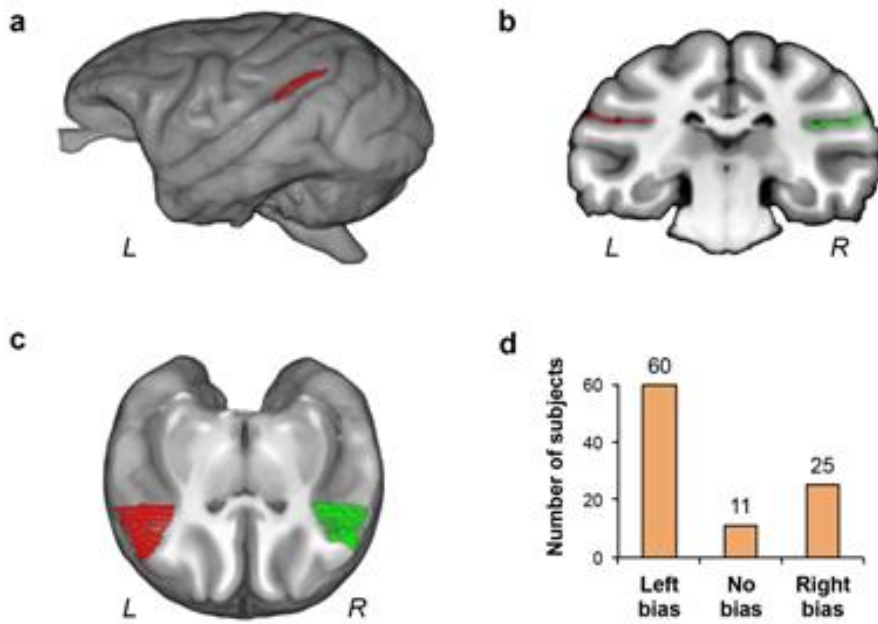
Fig. 2. — An female adult baboon tries to draw the attention of her offspring toward the piece of fruit that she waves between her fingers. This is the first time that such a “joint attention” gestural behavior has been observed in this species. ©Laboratoire de Psychologie Cognitive, CNRS, Univ. Aix-Marseille.



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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).