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On the Gestural Origin of Language Lateralisation: Manual Communication reflects Broca's Asymmetry in Monkeys

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Manual gestures and speech recruit a common neural network, involving Broca area in the left hemisphere. Evolutionary questions about this language organization led to a renewed attention for comparative research on gestural communication in our closer primate relatives and its potential language-like features. Here, using in vivo anatomical MRI in 80 baboons, we found that communicative gesturing's lateralisation – but not handedness for manipulation - is related to Broca homologue's marker in monkeys, namely contralateral depth hemispheric asymmetry of the ventral portion of the inferior arcuate sulcus. This finding provides strong support for the gestural evolutionary continuities with language-related frontal specialization, dating back not only to *Homo sapiens* evolution, but rather to a much older common ancestor shared with old-world monkeys, 25-35 million years ago.

Background:

Broca area and its left hemispheric specialization, has historically been considered as the centre of speech production¹. Even if such a modular conception of language neural bases was questioned by models of plastic and large distributed networks¹, it is still well acknowledged that Broca area

29 in the left hemisphere remains a key node for language specialization within this neural distributed
30 network. Complementary work thereby highlighted Broca area as an interface between speech
31 and multimodal motor integration including gesture and mouth movements². Broca area is also
32 known for its involvement in motor planning, sequential and hierarchical organization of
33 behaviours, such as linguistic grammar or tool use and tool making²⁻⁴. This body of work raises
34 evolutionary questions about the role of the motor system and gestural communication in language
35 origins and its brain specialization. Therefore, a growing number of researchers proposed that
36 language organization took some of its phylogenetical roots into a gestural system across primate
37 evolution^{2,5,6}.

38 Consequently, whereas comparative research has focused on the potential continuities between
39 language organisation and the vocal and auditory system in nonhuman primates⁷, the research on
40 gestural communication in apes and monkeys has recently received an increased interest within
41 this evolutionary framework. A large body of primate studies have documented some gestural
42 continuities with several key features of human language such as intentionality, referentiality,
43 learning flexibility and lateralisation^{6, 8, 9}. About this latter feature, primate studies have indeed
44 shown a specific pattern of manual lateralisation for communicative gestures in comparison to
45 handedness for non-communicative actions: namely in baboons, chimpanzees and even humans,
46 the use of the right hand tend to increase for communicative gestures specifically, even in left
47 handed individuals⁹. In other words, primates can independently be classified as left- or right-
48 handed for communicative gesture or non-communicative actions⁹. Those behavioural findings in
49 different primate species suggested a specific left-hemisphere specialisation for communicative
50 gestures, which might be different from handedness. Given handedness in humans turned out to
51 be a poor marker of hemispheric specialization for language in contrast to communicative gesture⁹,

52 some authors have proposed that such a specific lateralised gestural system found in nonhuman
53 primates might reflect evolutionary continuities with frontal hemispheric specialisation for
54 speech/gesture integration⁹. However, this hypothesis suffers from the critical lack of data in our
55 closer primate relatives on the brain correlates of communicative gestures' lateralisation.
56 Interestingly, like in humans, gross left-hemispheric asymmetries of homologous language areas
57 were also found in nonhuman primates. In particular Broca homologue in great apes¹⁰ and the
58 Planum Temporale in both great apes and baboons, an Old World monkey species^{11,12}.
59 For Old World monkeys, no structural asymmetry for Broca homologue has been reported so far.
60 One reason is that determining this area in monkeys is particularly challenging in comparison to
61 apes. In fact, the inferior precentral sulcus, the inferior frontal sulcus and the fronto-orbital sulcus,
62 which are common borders of Broca homologue in apes⁸, are absent in monkeys and thus
63 delimitation is not trivial.
64 Nevertheless, all the detailed cytoarchitectonic studies addressing the Broca homologue within the
65 frontal lobe in Old World monkeys (i.e. in mostly macaques but also in baboons) - and its two
66 components Area 44 and 45 - pointed towards the same sulcus of interest as the epicentre of this
67 region: the mid-ventral and ventral portion of the inferior arcuate sulcus (*IA sulcus*). The *IA sulcus*
68 is considered homologue to the ascending branch of the inferior precentral sulcus¹³, which delimits
69 Broca area posteriorly in humans and great apes. In monkeys, Area 45 homologue sits in the
70 anterior bank of the ventral *IA sulcus*¹⁴. In contrast, Area 44 homologue might be located in the
71 fundus and the posterior bank of the ventral *IA sulcus* in monkeys¹⁴, which overlaps with F5 region
72 related to the mirror neuron system^{15,16}. In fact, electric stimulation in the fundus of the ventral *IA*
73 *sulcus* elicited oro-facial and finger movements in macaques¹⁴. Concerning baboons specifically,
74 a cytoarchitectonic study¹⁷ showed similarities to the macaque frontal lobe organisation given Area

75 45 anteriorly to the *IA sulcus*, even if Area 44 was not described¹⁴⁻¹⁷. Therefore, in the absence of
76 the usual Broca's sulcal borders found in apes, the depth of the ventral part of the *IA sulcus*
77 constitutes the only critical neuroanatomical marker for delimiting the border and the surface of
78 Broca homologue in monkeys.

79 In the present MRI study conducted in an initial population of 80 in vivo baboons (*Papio anubis*),
80 we have (1) measured the inter-hemispheric asymmetries of the *IA sulcus*' depth - from its dorsal
81 to its most ventral portion (2) as well as its potential behavioural correlates (communicative
82 gesture's lateralisation versus handedness) among the baboons for which data was available for
83 hand preference for communicative gestures (n=58) and handedness for non-communicative
84 manipulative action (N=71).

85 To evaluate the hypothesis of an evolutionary continuity between the communicative gesture's
86 lateralised system in baboons and frontal hemispheric specialization for language⁹, we tested
87 specifically whether the depth asymmetry of the most ventral IA portion – the Broca homologue
88 – was exclusively associated with communicative gestures' lateralisation.

89

90 **Methods:**

91 Subjects:

92 Inter-hemispheric asymmetries of the *IA sulcus*' depth were quantified from anatomical T1w MRI
93 images in 80 baboons *Papio anubis* born in captivity and free from developmental or anatomical
94 abnormalities or brain disorders (generation F1, 52 females, 28 males, age range = 7 to 32 years,
95 mean age (years): M = 17,7 SE = 5,9). Out of this sample, 4 subjects did not present any
96 behavioural data and were thus excluded from further analyses, 53 baboons had individual
97 measures for both hand preference for communicative gestures and for handedness for

98 manipulative actions, 5 had only for communicative gestures and 18 only for manipulative actions.
99 In total, 58 baboons were then included in the “communication” hand preference group (36 females
100 and 22 males, mean age (years): $M = 17.9$, $SE = 6.2$) and 71 in the “action” handedness group (44
101 females and 27 males, mean age (years): $M = 17.6$, $SE = 5.6$).

102 All baboons were housed in social groups at the Station de Primatologie CNRS (UPS 846, Rousset,
103 France; Agreement number for conducting experiments on vertebrate animals: D13-087-7) and
104 have free access to outdoor areas connected to indoor areas. Wooden and metallic, ethologically
105 approved, structures enrich the enclosures. Feeding times are held four times a day with seeds,
106 monkey pellets and fresh fruits and vegetables. Water is available ad libitum. The experimental
107 procedure complied with the current French laws and the European directive 86/609/CEE.

108

109 Sulcal Parametrization:

110 The *IA sulcus* was extracted from T1w images using the pipeline of the free BrainVisa software
111 (see ¹³ for details of the procedure). The sulcus parametrization tool within the BrainVisa toolbox
112 provides therefore sulcus-based morphometry by subdividing the *IA sulcus* of each hemisphere
113 into 99 standardized positions from dorsal to ventral sulcus extremities in order to quantify the
114 variation of sulcal depth all across the *IA sulcus*' 99 positions²². To estimate asymmetries of the
115 *IA sulcus* depth between the two hemispheres an asymmetry quotient (AQ) for each of the 99 sulcal
116 positions ($AQ = (R - L) / [(R + L) \times 0.5]$) was computed¹².

117

118 Behaviour Correlate:

119 For further investigating its potential behavioural correlates, we tested whether the right- versus
120 left-handed groups classified for a given manual task (i.e., gestural communication versus

121 manipulative actions) differed in term of neurostructural depth asymmetries (AQ) within the *IA*
122 *sulcus*.

123 Hand preference for communicative gesture was previously assessed in a sample of 58 baboons.

124 Communicative gesture was defined as a movement of the hand directed to a specific partner or

125 audience in order to affect its behaviour²³. Similarly, than apes, some communicative manual

126 gestures in baboons have been found to share intentional control, referential properties, flexibility

127 of acquisition and of use as well as similar specific pattern of manual lateralisation (reviewed in ¹⁵

128 and ⁷). The present study focused specifically on the “Hand slapping” gesture which was

129 previously found optimal for measuring gestural communication’s lateralisation in this species⁹.

130 Indeed the hand slapping behaviour - used by the baboon to threat or intimidate the recipient - is

131 the most common and frequent visual gesture of the repertoire²³ produced intentionally and

132 unimanually in a lateralised manner across similar agonistic contexts and similar emitter’s

133 postures⁹. Hand use was recorded in a baboon when slapping or rubbing quickly and repetitively

134 the hand on the ground in direction to a conspecific or a human observer at an out of reach distance.

135 Handedness for manipulative actions was assessed among a sample of 71 baboons using the well-

136 documented bimanual coordinated “Tube task”⁹. Hand use was recorded when extracting food

137 with a finger out of a PVC tube hold by the other hand (see ⁷ for full details of the hand preference’s

138 data collection procedure).

139 The individual handedness index (HI) for a given manual behavior, or degree of individual manual

140 asymmetry, was calculated based on the formula $(\#R - \#L) / (\#R + \#L)$, with #R indicating right hand

141 responses and #L for left hand responses. The HI values vary between -1 and +1 with positive

142 values indicating right hand preference and negative values indicating left hand preference.

143

144 Statistical analysis:

145 Statistical analysis was conducted using R 3.6.1 by Cluster Mass Permutation tests¹⁸.

146 First, an assembly of depth asymmetry measures was defined as a “cluster” when continuous
147 significant differences of the same sign across positions were found between groups (two-sided t-
148 tests, Welch corrected for inequality of variance, $p < .05$). Second, the sum of t-values within each
149 cluster was calculated (the “cluster mass”).

150 Next, permutations were conducted for the between individual tests: L and R values were randomly
151 redistributed between individuals (not between cuts) and the maximum absolute cluster mass was
152 calculated for each randomly permuted set. This procedure was repeated 5000 times and the 99%
153 confidence interval (CI) of the maximum cluster mass was calculated. The clusters in the observed
154 data were considered significant at 1% level if their absolute cluster mass was above or below the
155 99% CI of the distribution (i.e. $p > .01$).

156 We also performed a linear correlation between (1) the Handedness Index (HI) values for
157 communicative gesture calculated from the 58 individuals and (2) the Asymmetric Quotient (AQ)
158 values of those 58 baboons calculated from the respective left and right IA sulcus’ depth sum of
159 the continuous positions of the cluster for which a significant difference in AQ score (if any) is
160 detected by t-test comparison between the right- and left-handed groups. The same procedure was
161 followed for the HI values for non-communicative actions. No significant correlation was found
162 for the non-communicative action analysis.

163

164 **Data availability**

165 The behavioural, neuro-anatomical and statistic code data that support the findings of this study

166 are available in “OSF Storage” with the identifier DOI 10.17605/OSF.IO/DPXS5.

167 <https://mfr.osf.io/render?url=https%3A%2F%2Fosf.io%2Fngwx3%2Fdownload>

168

169 **Results:**

170 Between baboons communicating preferentially with the right hand versus the ones with the left
171 hand, we found significant contralateral differences of depth asymmetries in the ventral portion of
172 the *IA sulcus* (i.e., from the mid-ventral *IA* position to the most ventral *IA sulcus* portion, namely
173 from contiguous positions 65 to 97 out of the 99 segmented positions of the entire *IA sulcus*)
174 according to a cluster-based permutation test ($p < .01$)¹⁸. In other words, the 35 baboons using
175 preferentially their right hand for communicative gestures showed more leftward *IA sulcus* depth
176 asymmetry at this cluster than the 23 ones using preferentially their left-hand. In contrast, for non-
177 communicative manipulative actions, we found no difference of depth sulcus asymmetries
178 between the left- (N = 29) versus right-handed (N = 42) groups concerning any portion of the *IA*
179 *sulcus* ($p > .10$) (Fig. 1). Finally, there was significant negative correlation between
180 individual AQ depth values of the Broca’s cluster (i.e., from positions 65 to 97) and individual
181 hand preference’s degree for communication (HI) : $r(56) = -0.272$; $p < .05$ (i.e. stronger the hand
182 preference is for one hand, deeper is the IAS asymmetry from positions 65 to 97 in the contralateral
183 hemisphere). The AQ score per subject representing the depth asymmetry of the whole Broca’s
184 cluster was calculated from the sum of the IAS depths from positions 65 to 97 in the left
185 hemisphere and the sum of IAS depths from position 65 to 97 in the right hemisphere. The same
186 analysis on handedness for non-communicative actions was not significant.

187 Among the subsample of the common 53 subjects for which measures of hand preference for both
188 communicative gestures and non-communicative actions were available, further analysis

189 confirmed the same significant cluster of group difference at the identical ventral part of the *IA*
190 *sulcus* for gestural communication only, according to cluster-based permutation test ($p < .01$)
191 (figure in SI).

192 When comparing with a "control" sulcus of interest, the Central sulcus related to the primary motor
193 cortex, opposite effect was found between handedness for manipulative actions and hand
194 preferences for communicative gesture. In contrast to handedness for manipulation (see
195 Margiotoudi et al., 2019), no left-/right-handed group difference in the Central sulcus' depth
196 asymmetry (AQ) was found at any portion of the sulcus for communicative gesture (figure in SI).

197

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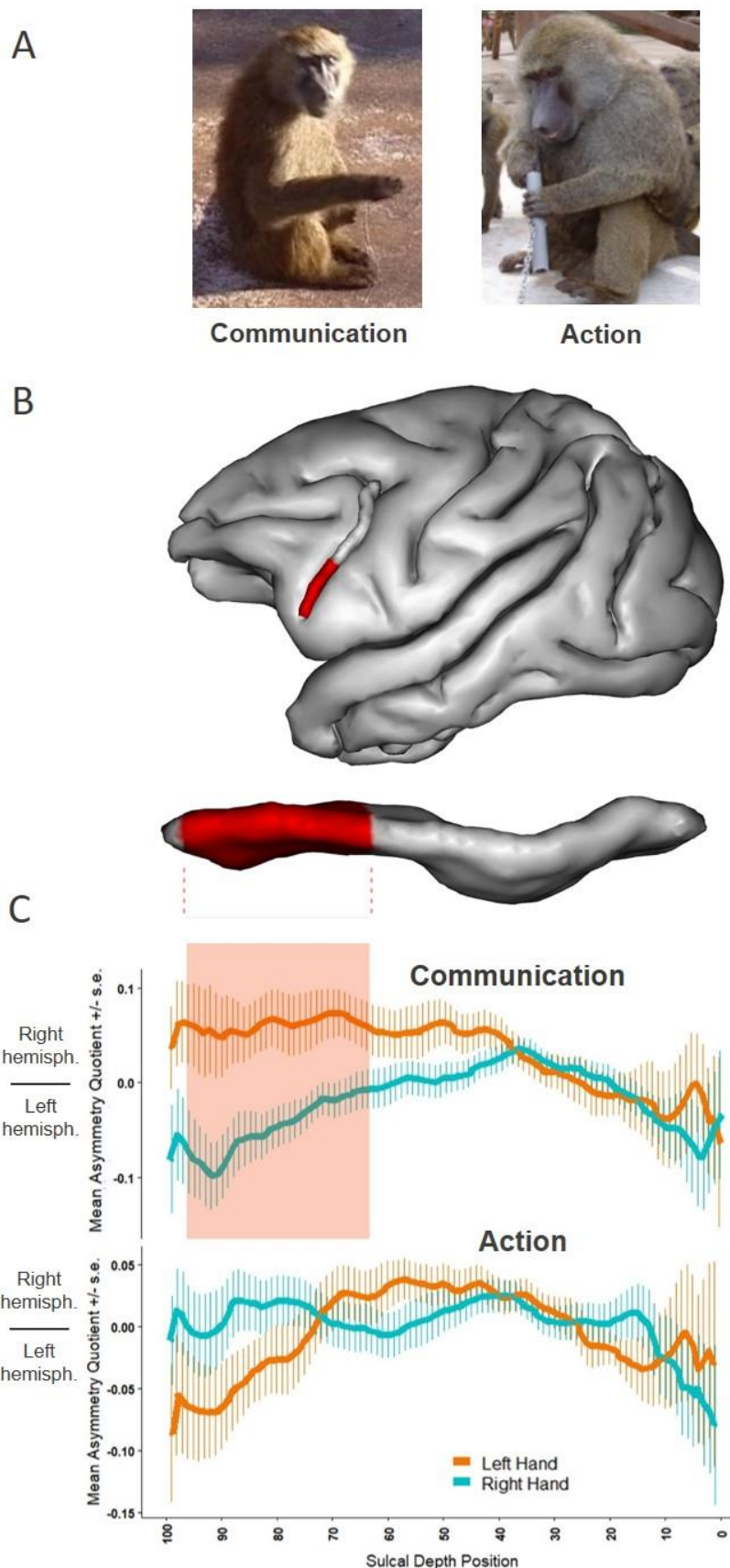


Figure 1: Example of quantified gestures (A), neuroanatomical location of the ROI (B) and asymmetry graphs (C).

A) Pictures of baboons. “Communication”: a “Handslap” communicative gesture in a juvenile male “Action”: the non-communicative bimanual coordinated “tube task” performed by an adult male.

(B) 3-D brain representation from BrainVisa software of the baboon’s left hemisphere, including the *IA sulcus* and its most ventral portion in red.

(C) *IA sulcus* depth’s asymmetry from ventral to dorsal portions respectively for the two groups of baboons (right- in blue versus left-hand dominant in orange) classified according to their hand preference for communicative “Handslap” gesture, non-communicative bimanual coordinated actions.

Positive Mean Asymmetry Quotient values indicate rightward hemispheric asymmetry, negative Mean Asymmetry Quotient values leftward hemispheric asymmetry. \pm SE indicated the Standard Error. Highlighted in red, significant difference between the two groups was found only in the “communication” condition for a cluster including positions 65 to 97 ($p < .01$)

238 **Discussion:**

239 The results of the study are straightforward. As predicted, we showed that the *IA sulcus* asymmetry
240 at its mid-ventral and ventral portion (labelled as the “Broca cluster”) is associated exclusively
241 with both degree and direction of contralateral communicative manual gestures’ lateralisation in
242 baboons but not handedness for non-communicative actions.

243 In addition, as revealed by the significant negative correlation between the Handedness Index (HI)
244 values for gestures and the Asymmetric Quotient (AQ) depth values of the *IA sulcus* “Broca
245 cluster”, hand preference for gestural communication and contralateral depth asymmetries at the
246 most ventral portion of the *IA sulcus* seem to be related not only at a qualitative level but also at a
247 quantitative level as well. In other words, individuals with a higher degree of hand preference for
248 gestures have greater *IA sulcus* depth asymmetries at this ventral cluster in the hemisphere
249 contralateral to their preferred hand for communication.

250 The ventral positions of such sulcus depth asymmetries are clearly at a crossroad of Broca-related
251 frontal regions including the fundus of the sulcus, Area 44¹⁴, the anterior bank, Area 45¹⁴, the
252 posterior bank, ventral F5 or granular frontal area (GrF)^{15, 16}. Since the sulcus depth might reflect a
253 gyral surface and its underlying grey matter volume, future work of delineating and quantifying
254 grey matter of the ventral *IA sulcus* would help determining which of those sub-regions of the
255 Broca homologue is driving the asymmetry specifically.

256 Whereas handedness for manipulative actions in baboons was previously found related to the
257 motor cortex asymmetry within the central sulcus¹⁹, our present findings report the first evidence
258 in monkeys that the neurostructural lateralisation’s landmark of communicative gesture is located
259 in a frontal region, related to Broca homologue. Such a contrast of results between manipulation
260 and communication found at the cortical level are consistent with what was found at the

261 behavioural level in studies showing that communicative gesture in baboons and chimpanzees
262 elicited specific patterns of manual lateralisation in comparison to non-communicative
263 manipulative actions. Therefore, it provides strong support that gestural communication's
264 lateralisation in nonhuman primates might be related to a different lateralised neural system than
265 handedness for pure manipulative action. Its specific correlates with Broca homologue's
266 lateralisation is also consistent with what was found in our closest relatives, the chimpanzee^{20,21}.
267 It makes gestural communication a compelling embodied modality for one of the evolutionary
268 roots of the typical multimodal language system in humans and its left-hemispheric specialization.
269 Language-related frontal lateralisation might be much older than previously thought and inherited
270 from a gestural communicative system dating back, not to Hominid origins, but rather to the
271 common ancestor of humans, great apes and Old world monkeys, 25–35 million years ago.

272

273

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287

288 **Author contributions:** Y.B and A.M prepared the paper. Y.B performed the analyses. K.M., D.M.
289 prepared the MRI images pre-processing and sulcus extraction pipeline. M.R designed MRI
290 sequences, B.N. designed the baboons' monitoring programs, R.L. designed the specific
291 procedures of welfare, anaesthesia and preparation of baboons in the MRI machine J.L.A
292 supervised and coordinated the MRI sessions. O.C. designed the sulcus parametrization tool. N.C
293 designed the statistic procedure. A.M. supervised the study and MRI acquisitions.

294 **Competing interests:** Authors declare no competing interests.

295

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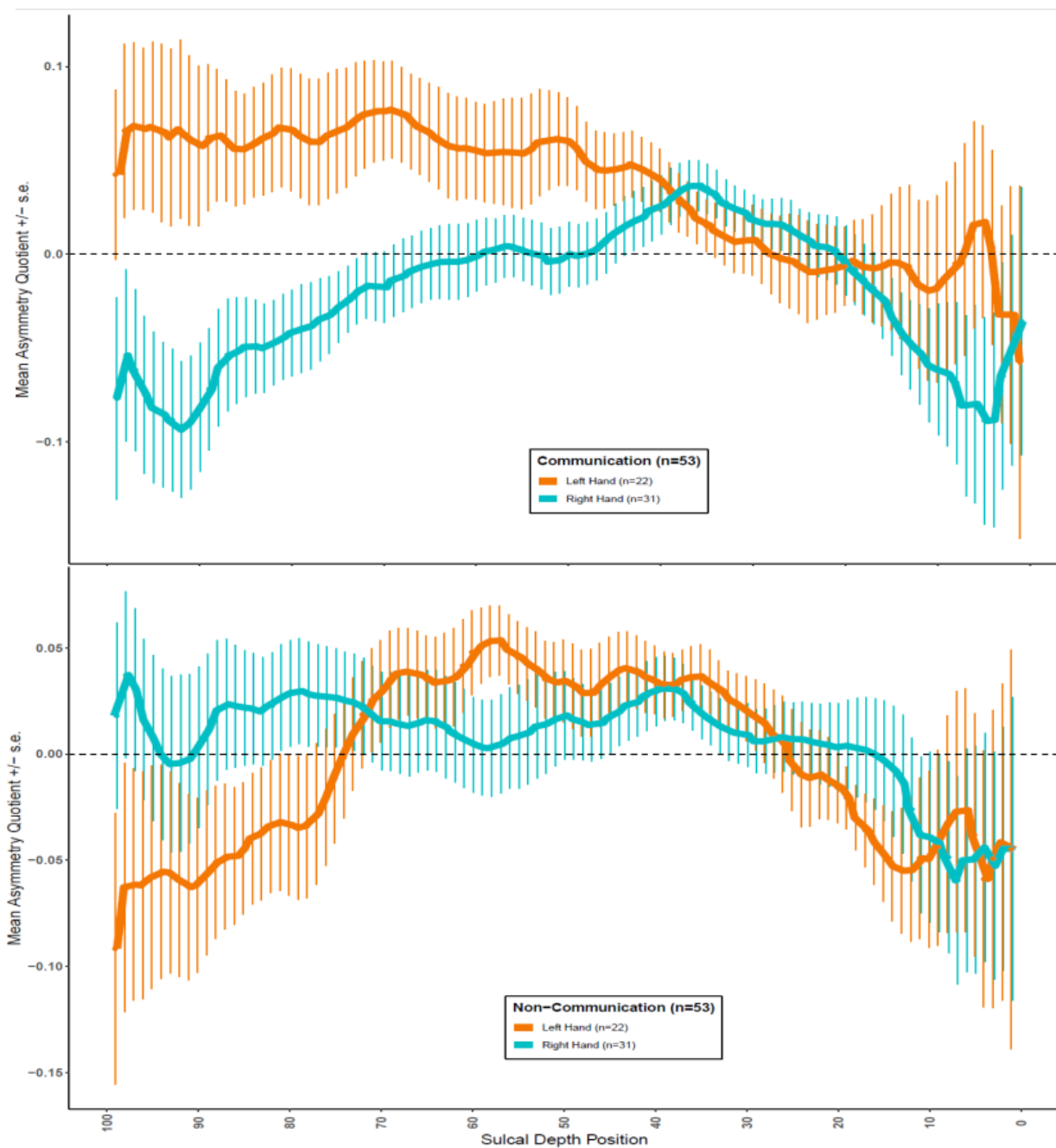
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362 **Supplementary Materials**

363 -Fig. S1: *IA sulcus* depth profile for the overlapping group (n= 53)

364 -Fig. S2: *Central sulcus* depth profile for communicative gesture (n= 63)

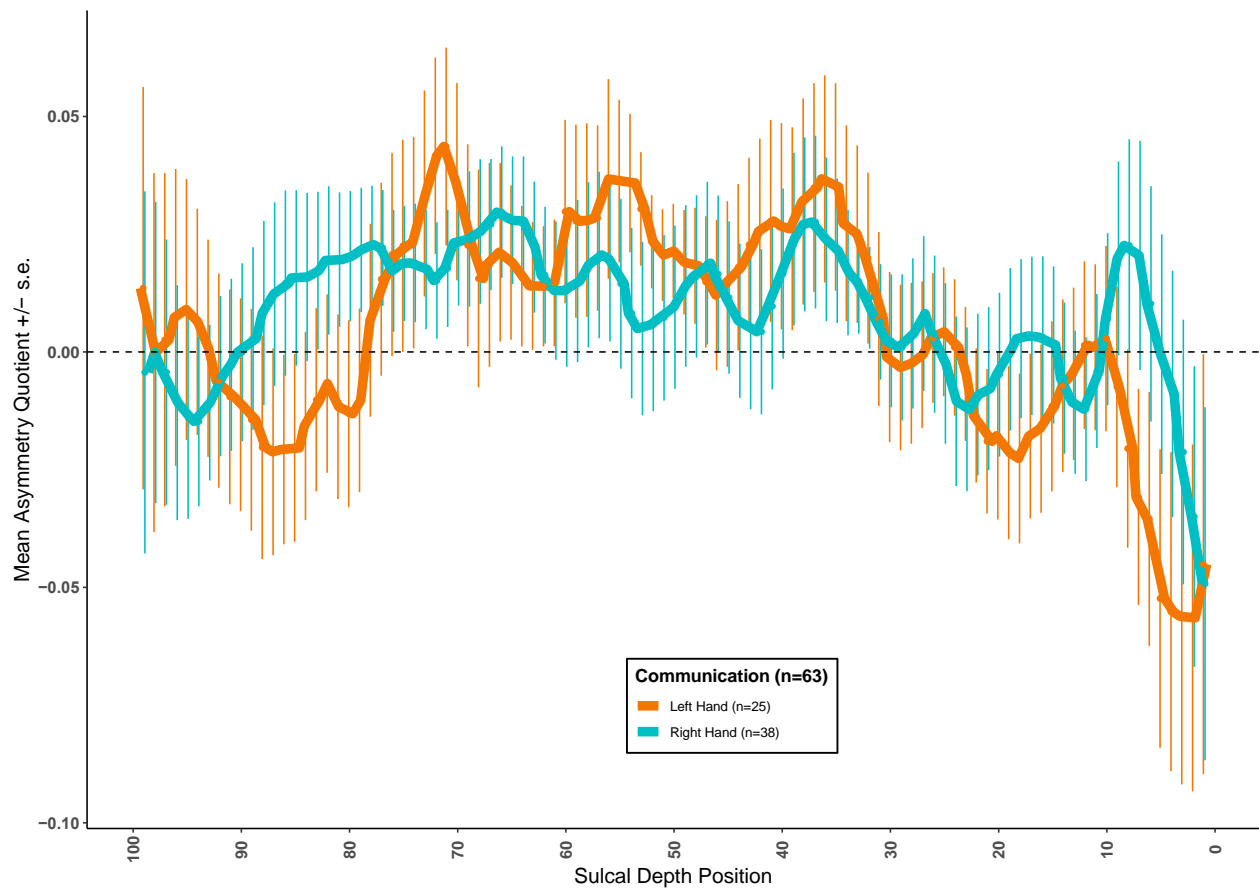


365 **Fig. S1: *IA sulcus* depth profile for the overlapping group (n= 53)**

366 A sulcus depth's asymmetry (AQ) from ventral to dorsal positions for 53 baboons (right- in blue versus left-hand
367 dominant groups in red) for which both communicative and non-communicative hand preference data were available.
368 A significant cluster of group difference is observed in the communicative gesture group ($p>0.01$), but no cluster in
369 the non-communicative gesture group.

370

371 **Fig. S2: Central sulcus depth profile for communicative gesture (n= 63)**



372

373 The Central Sulcus' depth asymmetry (AQ) from ventral to dorsal portions for 63 baboons (right- in blue versus left-
374 hand dominant groups in red). No cluster of group difference for communicative gesture can be observed. Data from
375 Margiotoudi 2019¹⁹.

A

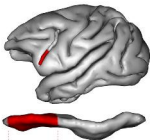


Communication



Action

B



C

