

1 **Broca area homologue's asymmetry reflects gestural communication**
2 **lateralisation in monkeys (*Papio anubis*)**
3

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12 **Abstract**

13 **Manual gestures and speech recruit a common neural network, involving Broca's area in**
14 **the left hemisphere. Such speech-gesture integration gave rise to theories on the critical**
15 **role of manual gesturing in the origin of language. Within this evolutionary framework,**
16 **research on gestural communication in our closer primate relatives has received renewed**
17 **attention for investigating its potential language-like features. Here, using *in-vivo***
18 **anatomical MRI in 50 baboons, we found that communicative gesturing-is related to Broca**
19 **homologue's marker in monkeys, namely the ventral portion of the Inferior Arcuate sulcus**
20 **(*IA sulcus*). In fact, both direction and degree of gestural communication's handedness –**
21 **but not handedness for object manipulation - are associated and correlated with**
22 **contralateral depth asymmetry at this exact *IA sulcus* portion. In other words, baboons**
23 **that prefer to communicate with their right hand have a deeper left-than-right *IA sulcus*,**
24 **than those preferring to communicate with their left hand and vice versa. Interestingly, in**
25 **contrast to handedness for object manipulation, gestural communication's lateralisation is**
26 **not associated to the *Central sulcus* depth asymmetry, suggesting a double dissociation of**
27 **handedness' types between manipulative action and gestural communication. It is thus not**

28 **excluded that this specific gestural lateralisation signature within the baboons' frontal**
29 **cortex might reflect a phylogenetical continuity with language-related Broca lateralisation**
30 **in humans.**

31

32 **Introduction**

33 Broca's area and its left hemispheric specialisation has historically been considered as the
34 centre of speech production (Friederici, 2017). Even if such a modular conception of language
35 neural bases was questioned by models of plastic and large distributed networks (Friederici,
36 2017; Hickok & Poeppel, 2007), it is still well acknowledged that Broca's area remains a key
37 node for language specialisation within this neural distributed network. Complementary work
38 thereby highlighted Broca's area as an interface between speech and multimodal motor
39 integration including gesture and mouth movements (Gentilucci & Volta, 2008). Broca's area is
40 also known for its involvement in motor planning, sequential and hierarchical organization of
41 behaviours, such as linguistic grammar or tool use and tool making (Gentilucci & Volta, 2008;
42 Koechlin & Jubault, 2006; Stout et al., 2015; Corballis, 2015; Wakita et al., 2014). This body of
43 work raises evolutionary questions about the role of the motor system and gestural
44 communication in language origins and its brain specialisation. Therefore, a growing number of
45 researchers proposed that language organization took some of its phylogenetical roots into a
46 gestural system across primate evolution (Gentilucci & Volta, 2008; Corballis, 2015; Tomasello,
47 2008). Consequently, whereas comparative language research has focused on the potential
48 continuities across primate brain circuitry (e.g., Balezeau et al., 2020; Becker et al., 2021a) or
49 vocal and auditory systems (e.g., Boe et al., 2017; Jarvis, 2019; Wilson et al., 2017), the research

50 on gestural communication in apes and monkeys has historically shown a significant interest
51 within this evolutionary framework.

52 A large body of non-human primate studies has documented some continuities of the
53 communicative gestural system with several key features of human language such as
54 intentionality, referentiality, learning flexibility and lateralisation (e.g., Tomasello, 2008;
55 Meguerditchian & Vauclair, 2014; Molesti et al., 2020). About manual lateralisation specifically,
56 studies in baboons and great apes have indeed showed that communicative manual gesturing
57 elicited stronger right-hand use in comparison to non-communicative manipulative actions at a
58 populational-level (reviewed in: Meguerditchian et al., 2013). In addition, at the individual level,
59 a double dissociation concerning the type of handedness has been documented between gestural
60 communication and object manipulation, showing that primates classified as right-handed for
61 communicative gesture are not especially classified as right-handed for object manipulation and
62 vice versa (Meguerditchian & Vauclair 2006, 2009). Those behavioural findings in different
63 primate species suggested a specific lateralized system for communicative gestures, which might
64 be different from the one involves in handedness for object manipulation. This is consistent with
65 human literature showing that typical object-manipulation handedness measures turned out to be
66 rather a poor marker of language lateralisation (Fagard, 2013), as most left-handers (78%) also
67 show left-hemisphere dominance for language (Knecht et al., 2000; Mazoyer et al., 2014), just
68 like right-handed people. In both humans and nonhuman primates, direction of handedness for
69 object manipulation were found associated to contralateral asymmetries of the motor hand area
70 within the *Central sulcus* (e.g., humans: Amunts, 2000; Cykowski et al., 2008; chimpanzees:
71 Hopkins & Cantalupo, 2004; Dadda et al., 2008; Baboons: Margiotoudi et al., 2019; Capuchin
72 monkeys: Phillips & Sherwood, 2005; Squirrel monkeys: Nudo et al, 1992). In fact, it has

73 recently been demonstrated that the neural substrates of typical handedness measures and
74 language brain organisation might be not related but rather independent from each other (Groen
75 et al, 2013; Ocklenburg et al, 2014; Häberling et al., 2016; Labache et al., 2020).

76 Whether gestural communication's handedness in humans is a better predictor of
77 language lateralisation and is thus different than typical handedness measures remain unclear.
78 Nevertheless, several studies in human are supporting this hypothesis. In early human
79 development, the degree of right-handedness for preverbal gestures is more pronounced at a
80 populational-level than handedness for manipulation (Blake et al., 1994; Bonvillian et al., 1997;
81 see also Fagard, 2013; Cochet & Vauclair, 2010) and increases when the lexical spurt occurs in
82 children contrary to manipulation handedness (Cochet et al., 2011). Moreover, further work
83 showed Broca activation in the left hemisphere also for sign language production including
84 manual and oro-facial gestures (Emmorey et al., 2004; MacSweeney, & Waters, 2008).

85 Given such potential lateralisation links between gesture and language in humans, it is
86 thus not excluded that the specific lateralisation's signature found for communicative gestures in
87 nonhuman primates might reflect evolutionary continuities with frontal hemispheric
88 specialisation for speech/gesture integration. This hypothesis might be relevant to investigate
89 given brain studies in nonhuman primates have shown human-like gross left-hemispheric
90 asymmetries of homologous language areas at a populational level: In particular Broca's
91 homologue in great apes (Cantalupo & Hopkins, 2001; Graïc et al., 2020) as well as the Planum
92 Temporale in great apes and even in baboons, an Old World monkey species, in both adult and
93 newborns (Gannon et al., 1998; Marie et al., 2018; Becker et al., 2021b,c).

94 For Old World monkeys specifically, no study regarding structural asymmetry for
95 Broca's homologue has been investigated. One reason is that determining this area in monkeys is

96 particularly challenging in comparison to apes. In fact, the inferior precentral sulcus, the inferior
97 frontal sulcus and the fronto-orbital sulcus, which are common borders of Broca's homologue in
98 apes (Cantalupo & Hopkins, 2001), are absent in monkeys and thus delimitation is not trivial.
99 Nevertheless, all the detailed cytoarchitectonic studies addressing the Broca's homologue within
100 the frontal lobe in Old World monkeys (i.e., in mostly macaques but also in baboons) - and its
101 two components Area 44 and 45 - pointed towards the same sulcus of interest as the epicentre of
102 this region: the mid-ventral and ventral portion of the inferior arcuate sulcus (*IA sulcus*). The *IA*
103 *sulcus* is considered homologue to the ascending branch of the inferior precentral sulcus (Amiez
104 & Petrides, 2009) which delimits Broca's area posteriorly in humans and great apes. In monkeys,
105 Area 45 homologue sits in the anterior bank of the ventral *IA sulcus* (Petrides et al., 2005). In
106 contrast, Area 44 homologue might be located in the fundus and the posterior bank of the ventral
107 *IA sulcus* in monkeys (Petrides et al., 2005), which overlaps with F5 region related to the mirror
108 neuron system (Belmalih et al., 2009; Rizzolatti et al., 2019). Electric stimulation in the fundus
109 of the ventral *IA sulcus* elicited oro-facial and finger movements in macaques (Petrides et al.,
110 2005). Concerning baboons specifically, a cytoarchitectonic study (Watanabe-Sawaguchi et al.,
111 1991) showed similarities to the macaque frontal lobe organisation given Area 45 anteriorly to
112 the *IA sulcus*, even if Area 44 was not described (Petrides et al., 2005; Belmalih et al., 2009;
113 Rizzolatti et al., 2019; Watanabe-Sawaguchi et al., 1991). Therefore, in the absence of the usual
114 Broca's sulcal borders found in apes, the depth of the ventral part of the *IA sulcus* constitutes the
115 only critical neuroanatomical marker for delimiting the border and the surface of Broca's
116 homologue in monkeys.

117 In sum, within the framework of the origin of hemispheric specialisation for language,
118 most comparative works in nonhuman primates focused on population-level asymmetry for

119 either brain or communicative behaviours. Those studies have reported similar population-level
120 leftward brain asymmetry for key language homologue regions (Gannon et al., 1998; Catalupo &
121 Hopkins, 2001; Marie et al., 2018; Becker et al., 2021b,c) or similar populational-level right-
122 handedness for communicative gestures (reviewed in: Meguerditchian et al., 2013).
123 Nevertheless, to test potential phylogenetic continuities, this approach suffered from lack of
124 studies investigating the direct behavioural/brain correlates at the individual-levels.

125 In the present *in-vivo* MRI study conducted in 50 baboons (*Papio anubis*), we have (1)
126 measured the inter-hemispheric asymmetries of the *IA sulcus*' depth - from its dorsal to its most
127 ventral portion among subjects for which the *Central sulcus* depth measure was available from a
128 previous study (Margiotoudi et al., 2019) (2) as well as its potential links with direction and
129 degree of communicative gesture's handedness in comparison to handedness for manipulative
130 actions as measured with a bimanual tube task (see Hopkins, 1995). In other words, we tested
131 specifically whether the depth asymmetry of the most ventral Inferior Arcuate sulcus' portion
132 (ventral *IA sulcus*, i.e., the Broca's homologue) - but not the *Central sulcus* - was exclusively
133 associated with communicative gestures' lateralisation.

134

135 **Results**

136 Between baboons communicating preferentially with the right hand *versus* the ones with
137 the left hand, we found significant contralateral differences of depth asymmetries in the ventral
138 portion of the *IA sulcus* (i.e., from the mid-ventral *IA* position to the most ventral *IA sulcus*
139 portion, namely from contiguous positions 65 to 95 out of the 99 segmented positions of the
140 entire *IA sulcus*) according to a cluster-based permutation test ($p < .01$, t-value clustermass=
141 76.16, for $p < .01$ a clustermass of 65.28 was needed, see Maris et al., 2007). In other words, the

142 28 baboons using preferentially their right hand for communicative gestures showed more
143 leftward *IA sulcus* depth asymmetry at this cluster than the 22 ones using preferentially their left-
144 hand. In contrast, for non-communicative manipulative actions, we found no significant
145 difference of depth sulcus asymmetries between the left- (N = 22) *versus* right-handed (N = 28)
146 groups concerning any portion of the *IA sulcus*, according to a cluster-based permutation test (p
147 $> .10$) (Fig. 1).

148 In addition, after calculating the AQ score per subject representing the sulcus depth
149 asymmetry of the whole “Broca’s cluster” (i.e., from the sum of the *IA sulcus* depths from
150 positions 65 to 95 in the left hemisphere and the sum of *IA sulcus* depths from position 65 to
151 95 in the right hemisphere), we found a significant negative correlation between individual AQ
152 depth values of the Broca’s cluster (i.e., from positions 65 to 95) and individual handedness
153 degree for communication (HI) : $r(48) = -.337$; $p < .05$ (i.e. stronger the hand preference is for
154 one hand, deeper is the *IA sulcus* asymmetry from positions 65 to 95 in the contralateral
155 hemisphere) (Fig. 2 A). In contrast, AQ depth values of the Broca’s cluster did not show
156 significant correlation with HI for non-communicative actions ($r(48) = -.037$; $p \approx 1$) (Fig. 2 B).
157 Using the cocor package in R (Diedenhofen, B. & Musch, J., 2015), a comparison between these
158 two overlapping correlations based on dependent groups showed a significant difference between
159 the two correlations ($p < .05$).

160 When comparing with the control sulcus of interest, the *Central sulcus* related to the
161 primary motor cortex, opposite effect was found between handedness for manipulative actions
162 and hand preferences for communicative gesture. We found no significant difference of sulcus
163 depth asymmetries regarding communicative gestures. In contrast, Margiotoudi et al., (2019)
164 reported that the CS presented a contralateral asymmetry at continuous positions 56-60 (labelled

165 as the “Motor-hand area’s cluster”) for non-communicative manipulative actions, after
166 permutation tests for correction (Fig. 1).

167 Finally, we conducted a mixed-model analysis of variance with AQs depth values for
168 the *IA sulcus* “Broca’s cluster” and for the *Central sulcus* “Motor hand area’s cluster” (AQ
169 derived from continuous positions 56-60, see Margiotoudi et al., 2019) serving as the repeated
170 measure while communication handedness (left- *versus* right-handed) and action handedness
171 (left- *versus* right-handed) were between-group factors. The mixed-model analysis of variance
172 demonstrated a significant main effect on the AQ scores for communication handedness ($F_{1,46} =$
173 $14.08, p < 0.01$) and for action handedness ($F_{1,46} = 4.1, p < 0.05$).

174

175 Figure 1: Effect of left-/right-hand direction of two handedness types (communication vs. action)
176 on neuroanatomical sulcus depth asymmetries (*IA sulcus* vs. *Central sulcus*).

177

178 *Left panel:* Pictures of the two types of handedness measures in baboons. “Communication
179 Handedness”: a “Handslap” communicative gesture in a juvenile male “Action Handedness”: the
180 non-communicative bimanual coordinated “tube task” performed by an adult male.

181 *Top panel:* 3-D brain representation from BrainVisa software of the baboon’s left hemisphere,
182 including the *IA sulcus* and the *Central sulcus* with the portion in purple where a significant
183 effect was found in Margiotoudi et al., 2019.

184 *Graphs:* Sulcus depth’s asymmetry (AQ) comparison between right-handed group *versus* left-
185 handed group of baboons classified according to the type of manual tasks. Positive Mean
186 Asymmetry Quotient values (AQ) indicate rightward hemispheric asymmetry, negative Mean
187 Asymmetry Quotient values leftward hemispheric asymmetry. +/- SE indicated the Standard
188 Error.

189 (A) *IA sulcus* AQ between right-handed (N=28) *versus* left-handed (N=22) groups’ classification
190 for communicative “Handslap” gesture. Significant contralateral AQ difference ($p < .01$)
191 between the two groups was found for a cluster including positions 65 to 95 (highlighted in
192 purple in the graph and the 3D representation of the *IA Sulcus*).

193 (B) *Central Sulcus* AQ between right-handed (N=28) *versus* left-handed (N=22) groups’
194 classification for non-communicative bimanual coordinated actions.

195 (C) *IA sulcus* AQ between right-handed (N=28) *versus* left-handed (N=22) groups’ classification
196 for non-communicative bimanual coordinated actions.

197 (D) Initial graph (Adapted from Figure 2 from Margiotoudi et al., 2019) of the *Central Sulcus*
198 AQ showing the significant contralateral AQ differences ($p < .05$) found between the left-handed
199 (N=28) *versus* right-handed (N=35) groups group for the non-communicative bimanual

200 coordinated actions (Action condition) for positions 56 to 61 (highlighted in purple in the graph
201 and the 3D representation of the *Central Sulcus*).

202

203 Figure 2: Correlation between handedness degree types and the Broca's cluster's asymmetry

204 A. Individual handedness degree (HI) for communicative gestures and AQ depth values of the
205 Broca's cluster (i.e., from positions 65 to 95) in dark blue dots. Light blue line: Significant
206 negative correlation between HI and AQ.

207 B. Individual handedness degree (HI) for manipulative actions (HI) and AQ depth values of the
208 Broca's cluster (i.e., from positions 65 to 95) in dark green squares. Light green line
209 (superposing on x axis): Non-significant correlation between HI and AQ.

210

211

212 **Discussion**

213 The results of the study are straightforward. We showed that the IA sulcus left- or
214 rightward depth asymmetry at its mid-ventral and ventral portion (labelled as the "Broca
215 cluster") is associated exclusively with contralateral direction (left-/right-hand) of
216 communicative manual gestures' lateralisation in baboons but not handedness for non-
217 communicative actions. Building upon these first results, we also found a significant negative
218 correlation between the Handedness Index (HI) values for gestures and the Asymmetric Quotient
219 (AQ) depth values of the *IA sulcus* "Broca cluster", suggesting that the contralateral links
220 between handedness for gestural communication and depth asymmetries at the most ventral
221 portion of the *IA sulcus* is evident not only at a qualitative level but also at a quantitative level as
222 well. In other words, individuals with a stronger degree of manual lateralisation for
223 communicative gesture have greater *IA sulcus* depth asymmetries at this ventral cluster in the
224 hemisphere contralateral to their preferred hand for communication. The ventral positions of
225 such sulcal depth asymmetries are clearly at a crossroad of Broca-related frontal regions
226 including the fundus of the sulcus, Area 44 (Petrides et al., 2005), the anterior bank, Area 45
227 (Petrides et al., 2005), the posterior bank and ventral F5 or granular frontal area (GrF) (Belmalih

228 et al., 2009; Rizzolatti et al., 2019). Since the sulcus depth might reflect a gyral surface and its
229 underlying grey matter volume, future work of delineating and quantifying grey matter of the
230 ventral *IA sulcus* would help determining which of those sub-regions of the Broca homologue is
231 driving the asymmetry specifically, for instance by VBM methods.

232 Whereas handedness for manipulative actions in baboons was previously found related to
233 the motor cortex asymmetry within the *Central sulcus* (Margiotoudi et al., 2019), our present
234 findings report the first evidence in monkeys that the neurostructural lateralisation's landmark of
235 communicative gesture is located in a frontal region, related to Broca homologue. Such a
236 contrast of results between manipulation and communication found at the cortical level is
237 consistent with what was found at the behavioural level in studies showing that communicative
238 gesture in baboons and chimpanzees elicited specific and independent patterns of manual
239 lateralisation in comparison to non-communicative manipulative actions (Meguerditchian &
240 Vauclair, 2009; Meguerditchian et al., 2010). Therefore, it provides additional support to the
241 hypothesis suggesting that gestural communication's lateralisation in nonhuman primates might
242 be, just as language brain organisation in human (see Häberling et al., 2016), related to a
243 different lateralised neural system than handedness for pure manipulative action. Its specific
244 correlates with Broca homologue's lateralisation is also consistent with what was found in our
245 closest relatives, the chimpanzee (Tagliabata et al., 2006; Meguerditchian et al., 2012).

246 Regarding Broca's area in humans, very recently, a functional segregation was proposed
247 with Broca's anterior part implicated in language syntax and its posterior part exclusively
248 implicated in motor actions (Zaccarella et al., 2021). The authors argued that action and language
249 meet at this interface. In an evolutionary perspective we propose therefore that the intentionality
250 of primate's communicative gesture might account for this hypothesized functional interface of

251 actions and language prerequisites, nested inside the monkeys' Broca's homologue (see also:
252 Arbib 2006, Rizzolatti 2017, Corballis, 2015). In addition, in macaques Broca's homologue,
253 neuronal recordings showed populations of specific neurons activated for both volitional vocal
254 and manual actions (Gavrilov & Nieder, 2021).

255 The articulation of our results with this recent literature suggests that gestural
256 communication may be a compelling modality for one of the multimodal evolutionary roots of
257 the typical multimodal language system in humans and its hemispheric specialisation. It is thus
258 not excluded that language-related frontal lateralisation might be much older than previously
259 thought and inherited from a gestural communicative system dating back, not to Hominid
260 origins, but rather to the common ancestor of humans, great apes and Old World monkeys, 25–
261 35 million years ago.

262

263 **Methods**

264 Subjects

265 Inter-hemispheric asymmetries of the *IA sulcus*' depth were quantified from anatomical
266 T1w MRI images in 80 baboons *Papio anubis* born in captivity and free from developmental or
267 anatomical abnormalities or brain disorders (generation F1, 52 females, 28 males, age range = 7
268 to 32 years, mean age (years): $M = 17.7$, $SE = 5.9$). Out of this sample, were included only
269 subjects which overlaps with both (1) the sample of subjects for which individual measures of
270 handedness for communicative gestures were available (i.e., hand slapping gesture,
271 Meguerditchian & Vauclair, 2006) and (2) the previous sample of 63 subjects (i.e., 35 right-
272 handed and 28 left-handed) reported in Margiotoudi et al. (2019) for which both *Central sulcus*
273 depth measures and individual measures of handedness for manipulative actions (i.e. the

274 bimanual tube task, Vauclair et al., 2005) were reported. It resulted a total overlap of 50 baboons
275 (29 females and 21 males, mean age (years): $M = 12.3$, $SE = 5.8$) who combined thus the both
276 types of measures of handedness (communication *versus* manipulation) and the depth measures
277 of the two sulci of interest (*IA sulcus* and *Central sulcus*) in the two hemispheres of the brain.

278

279 All baboons were housed in social groups at the Station de Primatologie CNRS (UPS
280 846, Rousset, France; Agreement number for conducting experiments on vertebrate animals:
281 D13-087-7) and have free access to outdoor areas connected to indoor areas. Wooden and
282 metallic, ethologically approved, structures enrich the enclosures. Feeding times are held four
283 times a day with seeds, monkey pellets and fresh fruits and vegetables. Water is available ad
284 libitum. The study was approved by the “C2EA-71 Ethical Committee of Neurosciences” (INT
285 Marseille) under the number APAFIS#13553-201802151547729. The experimental procedure
286 complied with the current French laws and the European directive 86/609/CEE.

287

288 Sulcal Parametrization

289 The *IA sulcus* and the *Central sulcus* were extracted from T1w images using the pipeline
290 of the free BrainVisa software (see Mangin et al., 2004 for details of the procedure). The sulcus
291 parametrization tool within the BrainVisa toolbox provides therefore sulcus-based morphometry
292 by subdividing the *sulci* of each hemisphere into 99 standardized positions from dorsal to ventral
293 sulcus extremities in order to quantify the variation of sulcal depth all across the *sulci's* 99
294 positions (Mangin et al., 2004). This automatic algorithm is free from observer's judgment. To
295 estimate asymmetries of the *sulci's* depth between the two hemispheres an asymmetry quotient
296 (AQ) for each of the 99 sulcal positions ($AQ = (R - L) / [(R + L) \times 0.5]$) was computed

297 (Margiotoudi et al., 2019). The AQ values vary between -2 and +2 with positive values
298 indicating right-hemispheric lateralisation and negative values indicating left-hemispheric
299 lateralisation.

300

301 Behaviour Correlate

302 For further investigating its potential behavioural correlates, we tested whether the right-
303 *versus* left-handed groups classified for a given manual task (i.e., gestural communication *versus*
304 manipulative actions) differed in term of neurostructural depth asymmetries (AQ) within the *IA*
305 *sulcus* and the *Central sulcus*. The two types of handedness measures were previously collected
306 (for communicative gesture: Meguerditchian & Vauclair, 2006; Meguerditchian et al., 2011; and
307 for manipulative actions: Vauclair et al., 2005; Molesti et al., 2016).

308 Communicative gesture was defined as a mouvement of the hand directed to a specific
309 partner or audience in order to affect its behaviour (Molesti et al., 2020). Like in apes, some
310 communicative manual gestures in baboons have been found to share human-like intentional
311 control, referential properties, flexibility of acquisition and of use as well as similar specific
312 pattern of manual lateralisation (reviewed in Tomasello, 2008; Meguerditchian & Vauclair,
313 2014; Meguerditchian et al., 2013). The present study focused specifically on the “Hand
314 slapping” gesture which was previously found optimal for measuring gestural communication’s
315 lateralisation in this species (Meguerditchian & Vauclair, 2006, 2009; Meguerditchian et al.,
316 2011). Indeed, the hand slapping behaviour – a probably innate gestures used by the baboon to
317 threat or intimidate the recipient - is the most common and frequent visual gesture of the
318 repertoire (Molesti et al., 2020) produced intentionally and unimanually in a lateralised manner
319 across similar agonistic contexts and similar emitter’s postures (Meguerditchian et al., 2013).

320 Hand use was recorded in a baboon when slapping or rubbing quickly and repetitively the hand
321 on the ground in direction to a conspecific or a human observer at an out of reach distance.
322 Recorded events were taken from different bouts and not repeated measures from the same bout.
323 As in Margioudouti et al. (2019), in case a subject has been assessed in multiple sessions within
324 2004-2015, the final classification as right or left-handed was selected based on the session with
325 the most observations, excluding subjects with less than 5 observations (*Mean*=25.98,
326 *S.E.*=3.67).

327 Handedness for manipulative actions was assessed using the well-documented bimanual
328 coordinated “Tube task” (Hopkins, 1995). Hand use was recorded when extracting food with a
329 finger out of a PVC tube hold by the other hand.

330 The individual handedness index (HI) for a given manual behaviour, or degree of
331 individual manual asymmetry, was calculated based on the formula $(\#R-\#L)/(\#R+\#L)$, with #R
332 indicating right hand responses and #L for left hand responses. The HI values vary between -1
333 and +1 with positive values indicating right hand preference, negative values indicating left hand
334 preference and 0 indicating no preference. The absolute HI score indicate the strength of manual
335 preference.

336 Among the 50 baboons, for communicative gesture, 22 subjects were thus classified as
337 left-handed, 28 as right-handed following the HI direction. A 51th subject, having a HI score of 0
338 (i.e., no manual bias), could not be classified in either categories and has been thus excluded
339 from the study. For object-related manipulative actions (i.e., the bimanual tube task), 22 subjects
340 were classified as left-handed, 28 as right-handed as already reported in Margiotoudi et al.
341 (2019) for those 50 overlapping subjects. Among the 50 baboons, 18 subjects switched left-
342 /right-handed categories of hand preference between communicative gesture and manipulative

343 actions (i.e., 9 from left-handed group for gestural communication to right-handed group for
344 manipulative actions, 9 from right-handed group for gestural communication to left-handed
345 group for manipulative actions).

346

347 Statistical analysis

348 Statistical analysis was conducted using R 3.6.1 by Cluster Mass Permutation tests (Maris
349 et al., 2007). First, an assembly of depth asymmetry measures was defined as a “cluster” when
350 continuous significant differences of the same sign across positions were found between groups
351 (two-sided t-tests, Welch corrected for inequality of variance, $p < .05$). Second, the sum of t-
352 values within each cluster was calculated (the “cluster mass”). Next, permutations were
353 conducted for the between individual tests: For a given type of manual behaviour, Left-handed
354 individuals’ AQ values *versus* Right-handed individuals’ AQ values were randomly redistributed
355 between individuals and the maximum absolute cluster mass was calculated for each randomly
356 permuted set. This procedure was repeated 5000 times and the 99% confidence interval (CI) of
357 the maximum cluster mass was calculated. The clusters in the observed data were considered
358 significant at 1% level if their absolute cluster mass was above the 99% CI of the distribution
359 (i.e. $p < .01$).

360 We also performed a linear correlation between (1) the Handedness Index (HI) values for
361 communicative gesture calculated from the 50 individuals and (2) the Asymmetric Quotient
362 (AQ) values of those 50 baboons calculated from the respective left and right ventral *IA sulcus*’
363 depth sum of the continuous positions of the cluster for which a significant difference in AQ
364 score is detected by t-test comparison between the right- and left-handed groups. The same

365 procedure was followed for the HI values for non-communicative actions for those 50
366 individuals.

367

368 **Data availability**

369 The behavioural, neuro-anatomical and statistic code data that support the findings of this study
370 are available in “OSF Storage” with the identifier DOI 10.17605/OSF.IO/DPXS5.

371 https://osf.io/dpxs5/?view_only=f406ad972edd43e485e5e4076bae0f78

372

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388

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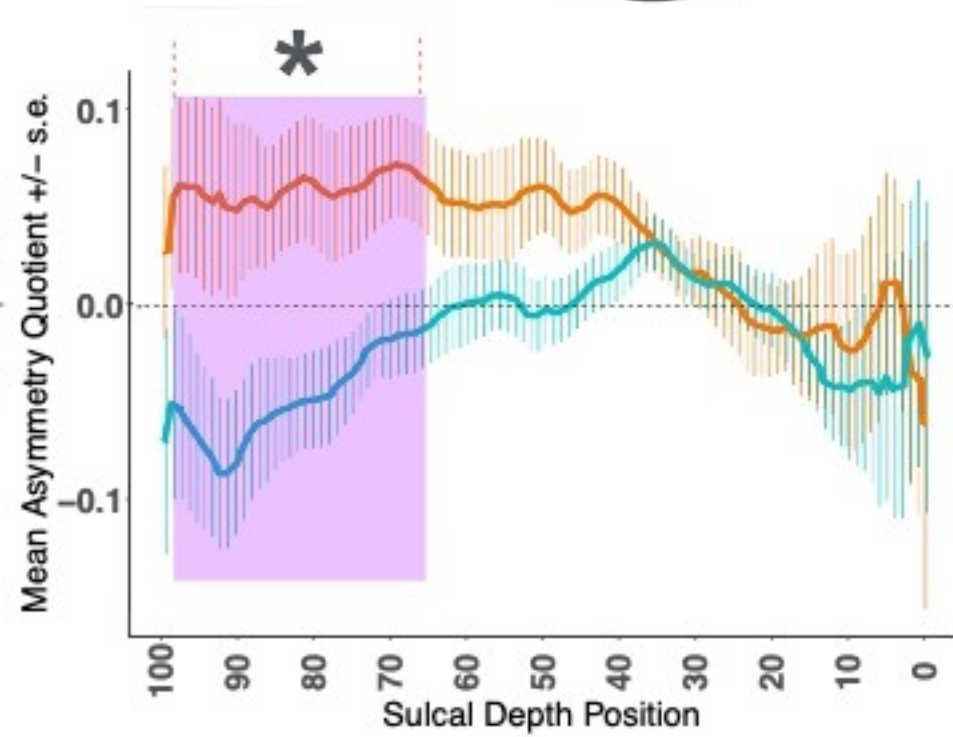
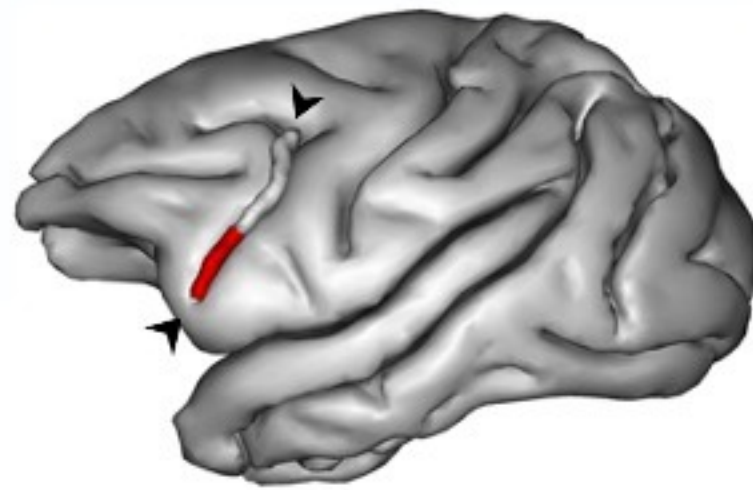
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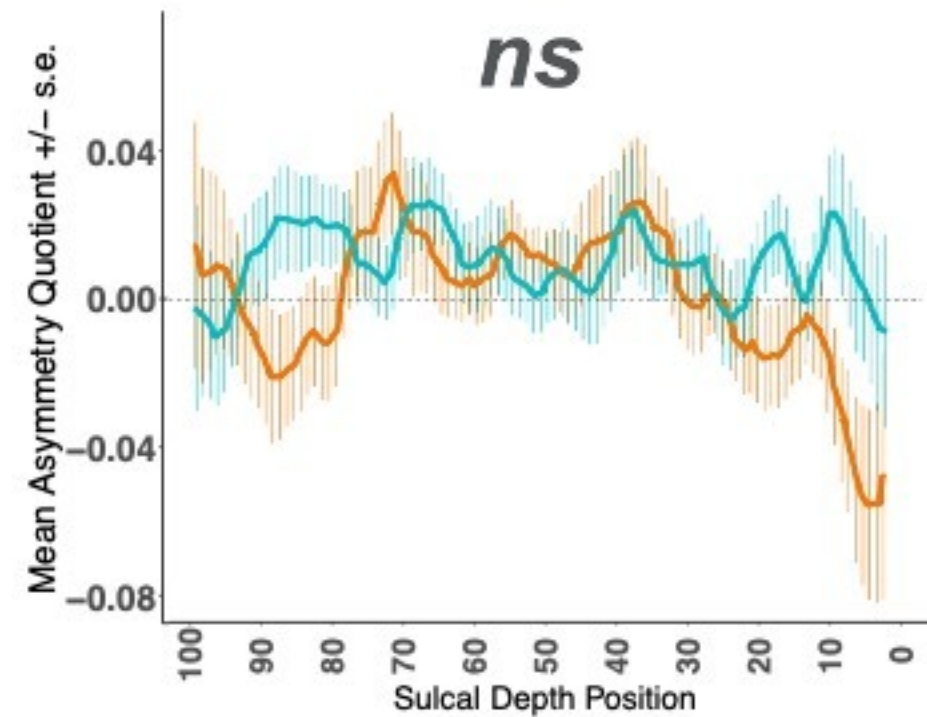
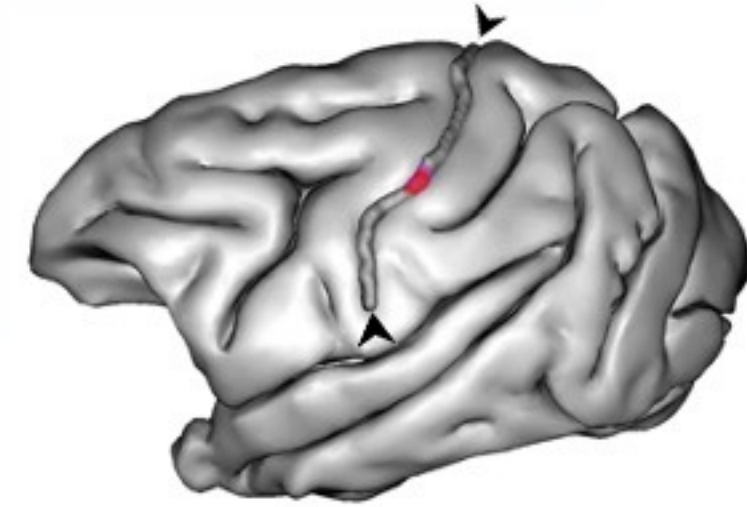
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562

ARCUATE SULCUS Broca's area



CENTRAL SULCUS Motor Cortex



COMMUNICATION Handedness



—+— Left-handed
—+— Right-handed

Right Hemisph.
Left Hemisph.

ACTION Handedness



—+— Left-handed
—+— Right-handed

Right Hemisph.
Left Hemisph.

