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 production[1]. Even if such a modular conception of language neural bases was questioned by models of plastic and large distributed networks[1], it is still well acknowledged that Broca area

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

Consequently, whereas comparative research has focused on the potential continuities between language organisation and the vocal and auditory system in nonhuman primates[7], the research on gestural communication in apes and monkeys has recently received an increased interest within this evolutionary framework. A large body of primate studies have documented some gestural continuities with several key features of human language such as intentionality, referentiality, learning flexibility and lateralisation[6, 8, 9]. About this latter feature, primate studies have indeed shown a specific pattern of manual lateralisation for communicative gestures in comparison to handedness for non-communicative actions: namely in baboons, chimpanzees and even humans, the use of the right hand tend to increase for communicative gestures specifically, even in left handed individuals[9]. In other words, primates can independently be classified as left- or right-handed for communicative gesture or non-communicative actions[9]. Those behavioural findings in different primate species suggested a specific left-hemisphere specialisation for communicative gestures, which might be different from handedness. Given handedness in humans turned out to be a poor marker of hemispheric specialization for language in contrast to communicative gesture[9],

some authors have proposed that such a specific lateralised gestural system found in nonhuman primates might reflect evolutionary continuities with frontal hemispheric specialisation for speech/gesture integration[9]. However, this hypothesis suffers from the critical lack of data in our closer primate relatives on the brain correlates of communicative gestures' lateralisation.

Interestingly, like in humans, gross left-hemispheric asymmetries of homologous language areas were also found in nonhuman primates. In particular Broca homologue in great apes[10] and the Planum Temporale in both great apes and baboons, an Old World monkey species[11,12].

For Old World monkeys, no structural asymmetry for Broca homologue has been reported so far. One reason is that determining this area in monkeys is particularly challenging in comparison to apes. In fact, the inferior precentral sulcus, the inferior frontal sulcus and the fronto-orbital sulcus, which are common borders of Broca homologue in apes[8], are absent in monkeys and thus delimitation is not trivial.

Nevertheless, all the detailed cytoarchitectonic studies addressing the Broca homologue within the frontal lobe in Old World monkeys (i.e. in mostly macaques but also in baboons) - and its two components Area 44 and 45 - pointed towards the same sulcus of interest as the epicentre of this region: the mid-ventral and ventral portion of the inferior arcuate sulcus (*IA sulcus*). The *IA sulcus* is considered homologue to the ascending branch of the inferior precentral sulcus[13], which delimits Broca area posteriorly in humans and great apes. In monkeys, Area 45 homologue sits in the anterior bank of the ventral *IA sulcus*[14]. In contrast, Area 44 homologue might be located in the fundus and the posterior bank of the ventral *IA sulcus* in monkeys[14], which overlaps with F5 region related to the mirror neuron system[15,16]. In fact, electric stimulation in the fundus of the ventral *IA sulcus* elicited oro-facial and finger movements in macaques[14]. Concerning baboons specifically, a cytoarchitectonic study[17] showed similarities to the macaque frontal lobe organisation given Area

45 anteriorly to the *IA sulcus*, even if Area 44 was not described[14-17]. Therefore, in the absence of the usual Broca's sulcal borders found in apes, the depth of the ventral part of the *IA sulcus* constitutes the only critical neuroanatomical marker for delimiting the border and the surface of Broca homologue in monkeys.

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

To evaluate the hypothesis of an evolutionary continuity between the communicative gesture's lateralised system in baboons and frontal hemispheric specialization for language[9], we tested specifically whether the depth asymmetry of the most ventral IA portion – the Broca homologue – was exclusively associated with communicative gestures' lateralisation.

Methods:

<u>Subjects:</u>

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

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

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

Sulcal Parametrization:

The *IA sulcus* was extracted from T1w images using the pipeline of the free BrainVisa software (see [13] for details of the procedure). The sulcus parametrization tool within the BrainVisa toolbox provides therefore sulcus-based morphometry by subdividing the *IA sulcus* of each hemisphere into 99 standardized positions from dorsal to ventral sulcus extremities in order to quantify the variation of sulcal depth all across the *IA sulcus*' 99 positions[22]. To estimate asymmetries of the *IA sulcus* depth between the two hemispheres an asymmetry quotient (AQ) for each of the 99 sulcal positions ($AQ = (R - L) / [(R + L) \times 0.5)$ was computed[12].

Behaviour Correlate:

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

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

Hand preference for communicative gesture was previously assessed in a sample of 58 baboons. Communicative gesture was defined as a movement of the hand directed to a specific partner or audience in order to affect its behaviour[23]. Similarly, than apes, some communicative manual gestures in baboons have been found to share intentional control, referential properties, flexibility of acquisition and of use as well as similar specific pattern of manual lateralisation (reviewed in [15] and [7]). The present study focused specifically on the "Hand slapping" gesture which was previously found optimal for measuring gestural communication's lateralisation in this species[9]. Indeed the hand slapping behaviour - used by the baboon to threat or intimidate the recipient - is the most common and frequent visual gesture of the repertoire[23] produced intentionally and unimanually in a lateralised manner across similar agonistic contexts and similar emitter's postures[9]. Hand use was recorded in a baboon when slapping or rubbing quickly and repetitively the hand on the ground in direction to a conspecific or a human observer at an out of reach distance. Handedness for manipulative actions was assessed among a sample of 71 baboons using the well-documented bimanual coordinated "Tube task"[9]. Hand use was recorded when extracting food with a finger out of a PVC tube hold by the other hand (see [7] for full details of the hand preference's data collection procedure).

The individual handedness index (HI) for a given manual behavior, or degree of individual manual asymmetry, was calculated based on the formula (#R-#L)/(#R+#L), with #R indicating right hand responses and #L for left hand responses. The HI values vary between -1 and +1 with positive values indicating right hand preference and negative values indicating left hand preference.

Statistical analysis:

Statistical analysis was conducted using R 3.6.1 by Cluster Mass Permutation tests[18].

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

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

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

Data availability

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

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

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

Results:

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

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

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

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

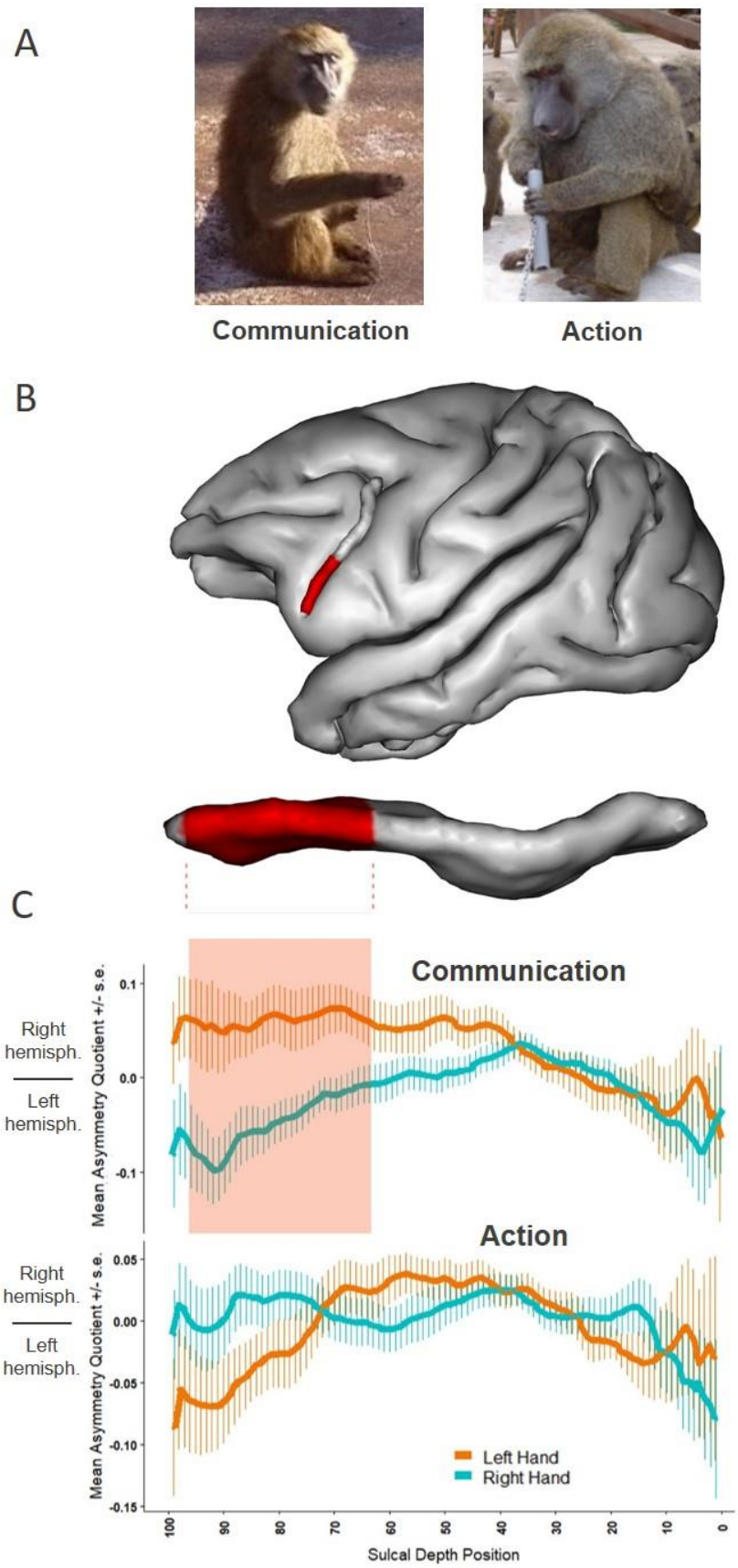

Figure 1: Example of quantified gestures (A), neuroanatomical location of the ROI (B) and asymmetry graphs (C).

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. +/- 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 ($p < .01$)

Discussion:

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

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

The ventral positions of such sulcus depth asymmetries are clearly at a crossroad of Broca-related frontal regions including the fundus of the sulcus, Area 44[14], the anterior bank, Area 45[14], the posterior bank, ventral F5 or granual frontal area (GrF)[15, 16]. Since the sulcus depth might reflect a gyral surface and its underlying grey matter volume, future work of delineating and quantifying grey matter of the ventral *IA sulcus* would help determining which of those sub-regions of the Broca homologue is driving the asymmetry specifically.

Whereas handedness for manipulative actions in baboons was previously found related to the motor cortex asymmetry within the central sulcus[19], our present findings report the first evidence in monkeys that the neurostructural lateralisation's landmark of communicative gesture is located in a frontal region, related to Broca homologue. Such a contrast of results between manipulation and communication found at the cortical level are consistent with what was found at the

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

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

Competing interests: Authors declare no competing interests.

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Supplementary Materials

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

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

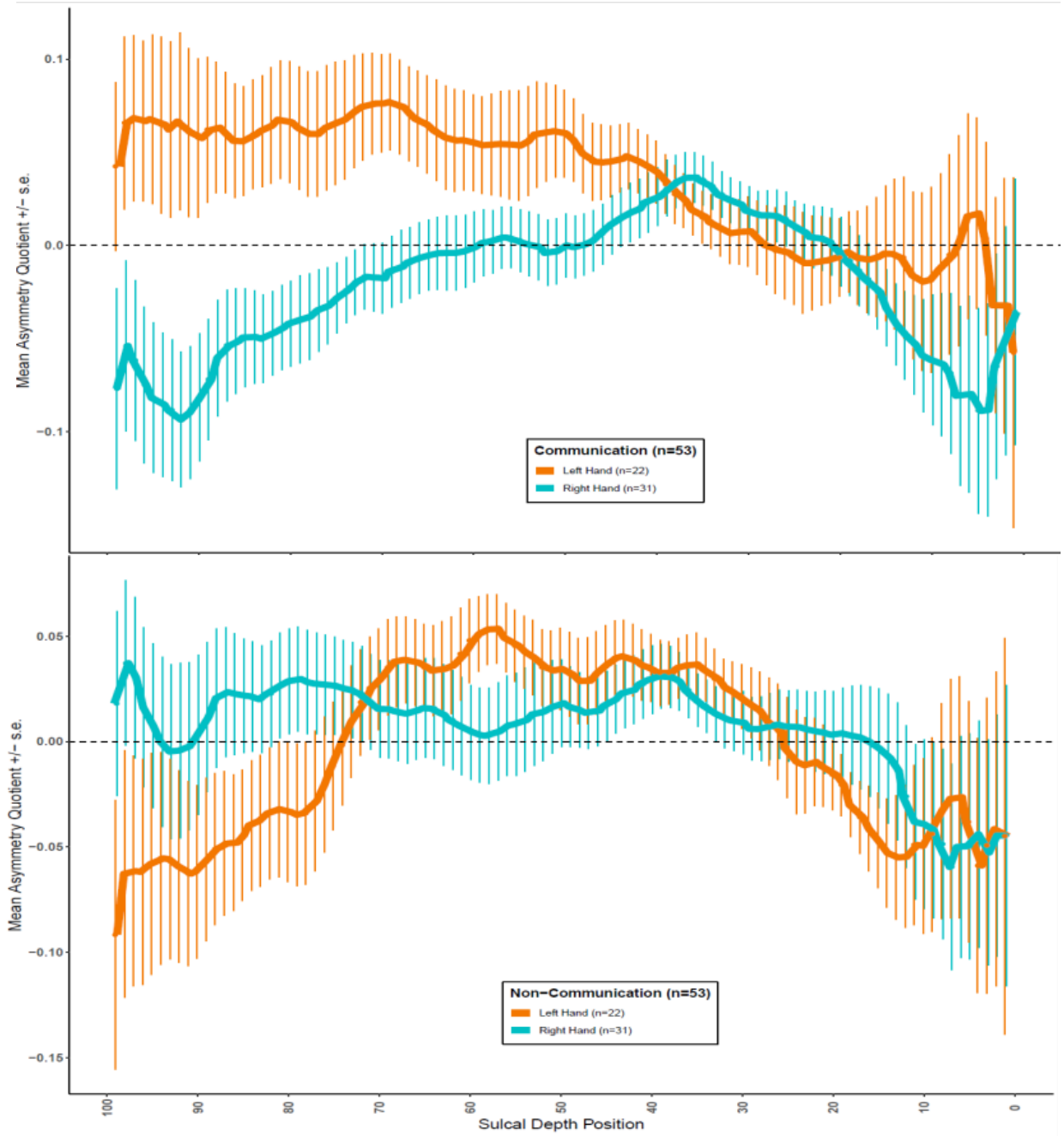
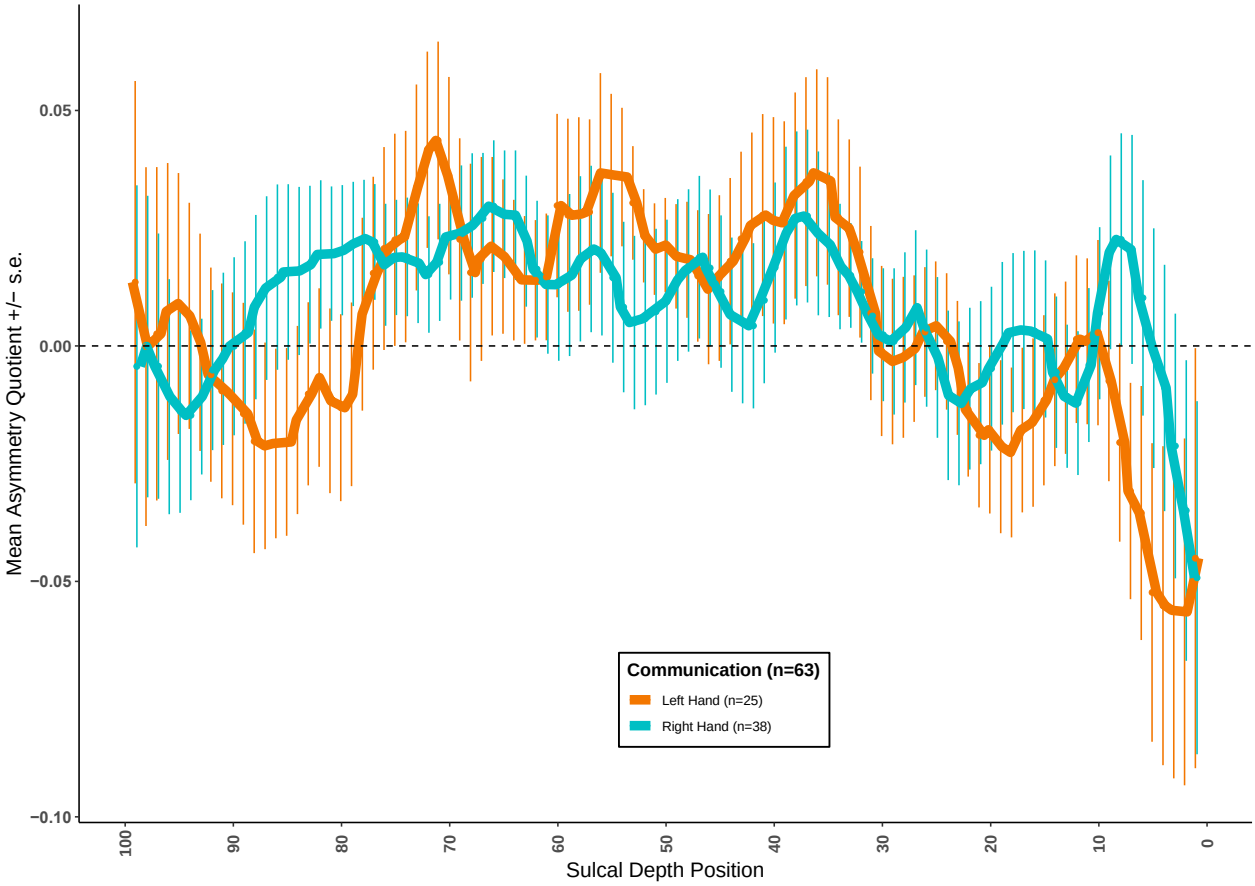


Fig. S1: *IA sulcus* depth profile for the overlapping group (n= 53)

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

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



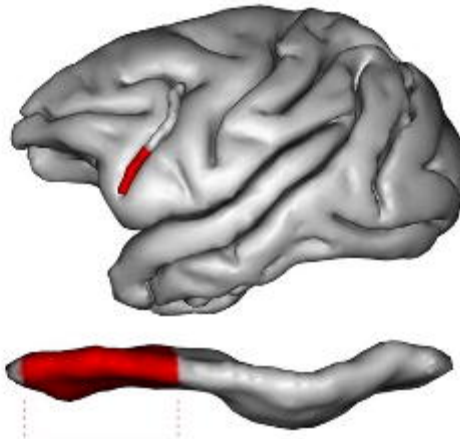
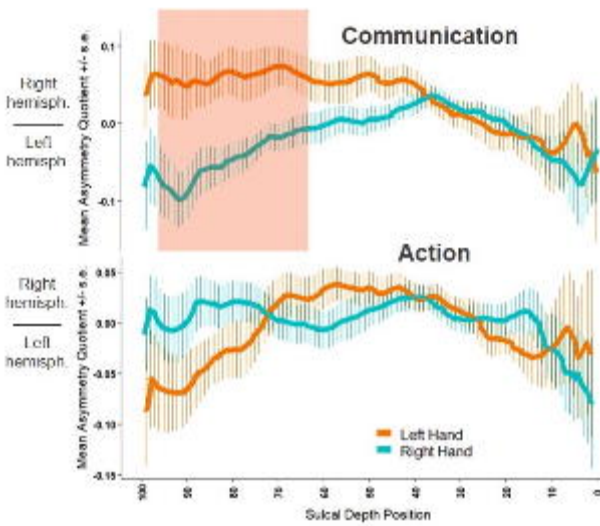
The Central Sulcus' depth asymmetry (AQ) from ventral to dorsal portions for 63 baboons (right- in blue versus left-hand dominant groups in red). No cluster of group difference for communicative gesture can be observed. Data from Margiotoudi 2019[19].

A

Communication

Action

B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