

Intraspecific gestural laterality in chimpanzees and gorillas and the impact of social propensities

Jacques Prieur, Simone Pika, Stéphanie Barbu, Catherine Blois-Heulin

► **To cite this version:**

Jacques Prieur, Simone Pika, Stéphanie Barbu, Catherine Blois-Heulin. Intraspecific gestural laterality in chimpanzees and gorillas and the impact of social propensities. *Brain Research*, Elsevier, 2017, 1670, pp.52 - 67. 10.1016/j.brainres.2017.05.033 . hal-01542694

HAL Id: hal-01542694

<https://hal-univ-rennes1.archives-ouvertes.fr/hal-01542694>

Submitted on 4 Sep 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Accepted Manuscript

Research report

Intraspecific gestural laterality in chimpanzees and gorillas and the impact of social propensities

Jacques Prieur, Simone Pika, Stéphanie Barbu, Catherine Blois-Heulin

PII: S0006-8993(17)30236-6

DOI: <http://dx.doi.org/10.1016/j.brainres.2017.05.033>

Reference: BRES 45382

To appear in: *Brain Research*

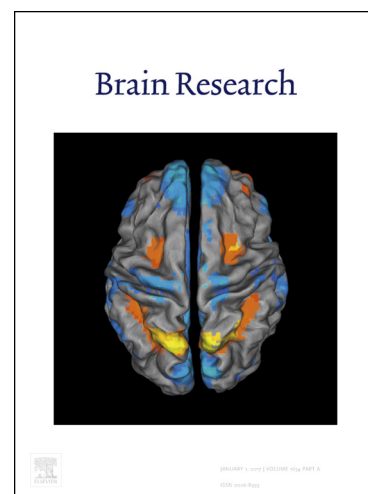
Received Date: 7 January 2017

Revised Date: 4 May 2017

Accepted Date: 31 May 2017

Please cite this article as: J. Prieur, S. Pika, S. Barbu, C. Blois-Heulin, Intraspecific gestural laterality in chimpanzees and gorillas and the impact of social propensities, *Brain Research* (2017), doi: <http://dx.doi.org/10.1016/j.brainres.2017.05.033>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.



Intraspecific gestural laterality in chimpanzees and gorillas and the impact of social propensities

Jacques Prieur^a, Simone Pika^{b, c}, Stéphanie Barbu^a, Catherine Blois-Heulin^a.

^a Ethos 'Ethologie Animale et Humaine', Université de Rennes 1–CNRS UMR 6552, Station biologique de Paimpont, France.

^b Max Planck Institute for Ornithology, Humboldt Research Group 'Evolution of communication', Seewiesen, Germany

^c Max Planck Institute for the Sciences of Human History, Department of Linguistic and Cultural Evolution, Humboldt Research Group, Jena, Germany

Correspondence: J. Prieur, UMR 6552, Station Biologique, Université de Rennes 1–CNRS, 35380 Paimpont, France. E-mail: jac.prieur@yahoo.fr

Abstract

A relevant approach to address the mechanisms underlying the emergence of the right-handedness/left-hemisphere language specialization of humans is to investigate both proximal and distal causes of language lateralization through the study of non-human primates' gestural laterality. We carried out the first systematic, quantitative comparison of within-subjects' and between-species' laterality by focusing on the laterality of intraspecific gestures of chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) living in six different captive groups. We addressed the following two questions: (1) Do chimpanzees and gorillas exhibit stable direction of laterality when producing different types of gestures at the individual level? If yes, is it related to the strength of laterality? (2) Is there a species difference in gestural laterality at the population level? If yes, which factors could explain this difference? During 1356 observation hours, we recorded 42335 cases of dyadic gesture use in the six groups totalling 39 chimpanzees and 35 gorillas. Results showed that both species could exhibit either stability or flexibility in their direction of gestural laterality. These results suggest that both stability and flexibility may have differently modulated the strength of laterality depending on the species social structure and dynamics. Furthermore, a multifactorial analysis indicates that these particular social components may have specifically impacted gestural laterality through the influence of gesture sensory modality and the position of the recipient in the signaller's visual field during interaction. Our findings provide further support to the social theory of laterality origins proposing that social pressures may have shaped laterality through natural selection.

Keywords: brain lateralization; handedness; conspecific-directed gestures; chimpanzees; gorillas; social factors.

1. Introduction

Brain functional lateralization refers to the lateral specialization of functions between the left and right cerebral hemispheres of the brain. Studies investigating brain laterality have shown hemispheric specializations for various functions including laterality in vision (e.g. Quaresmini et al. 2014), facial expression (e.g. Wallez et al. 2012), and both manipulative and communicative functioning (e.g. see McGrew & Marchant 1997 Meguerditchian et al. 2013 for reviews). For example, Meguerditchian and colleagues (2013) reviewed that humans and several species of non-human primate species exhibited a greater right-hand use in gestural communication than in non-communication actions. These findings thus indicate that gestures (from here, gestures are restricted to communication functions as defined by Pika & Bugnyar 2011) and non-communication functions would be related to different lateralized cerebral substrates. However, despite substantial research efforts into the cerebral structures and functions in human and non-human species (e.g. Knecht 2000; Hopkins et al. 2012; Ocklenburg & Gütürkün 2012; Häberling et al. 2016), mechanisms underlying brain functional lateralization are still unclear, even for human language related functions, although research devoted to language hemispheric specialization has received considerable attention since Broca's pioneering discovery (Broca 1865).

One of the reasons for this may be that the majority of human studies investigating language organization in the brain have naturally focused on verbal communication (spoken language). Moreover, although it is well established that the degree of language lateralization can vary across human subjects within a given verbal generation task (a commonly used activation task allowing the evaluation of expressive vocal communication: e.g. Knecht et al. 2000; Pirmoradi et al. 2016), only a few studies investigated how laterality can vary both within and between subjects across different verbal fluency tasks (e.g. Wilke et al. 2006, 2010). In addition to this, there is virtually no research investigating language lateralization both within and between subjects across different gestural generation tasks (i.e. through a comparison between various types of distinct expressed gestures to study the stability of the direction of laterality at both the individual and population levels). Complementary studies are thus required 1) to extend and deepen knowledge of the multimodal character of human language with regards to brain lateralization by further investigating gestural communication, 2) to study hemispheric specialization at both the individual and population levels for different communication activities, and 3) to continue the exploration of the ontogenetic and

phylogenetic mechanisms underpinning human brain lateralization for communication functions including gestural communication.

Research provided evidence that gestures play a crucial role in the communication of human and non-human primates (e.g. McNeill 1992; Call & Tomasello 2007; Pika 2012). In particular, it has been shown that apes and monkeys' gestural communication exhibit more intentionality and higher individual variability and flexibility than their vocal communication (e.g. Arbib et al. 2008; Meguerditchian & Vauclair 2014). Although a growing number of authors supports the multimodal origins of language, many of them (e.g. Gentilucci & Corballis 2006; Meguerditchian & Vauclair 2014) postulate that gestural communication would be the phylogenetic precursor of human left-lateralized intentional communication system. According to these authors, this system would have then gradually included intentional vocalizations and oro-facial expressions to elaborate the multimodal nature of our language.

A relevant approach to better identify the proximate and distal causes of language lateralization is the evolutionary comparative approach that investigates gestural laterality of humans' closest phylogenetic relatives, the non-human primates. To apply this approach, it is especially important to take into account socio-ecological validity (i.e. to consider situations close to those where natural selection has and/or is still acting) and thus to favor the investigation of naturally occurring intraspecific gestural communication in non-human primates. To date, however, only a few studies have examined gestural laterality in non-human primates during spontaneously occurring communicative interactions between conspecifics. Among these studies, only those of Chapelain (2010), Hobaiter and Byrne (2013) and Prieur and colleagues (2015, 2016a) have examined the effect of potentially influential factors on purely intraspecific gestural laterality. For instance, by using a multifactorial approach, Prieur and colleagues (2015, 2016a) recently showed that chimpanzees' intraspecific gestural laterality differed in relation to distinct gestural characteristics (e.g. sensory modality), interactional context components (e.g. emotional valence of the context), and individual socio-demographic characteristics of signaller and recipient (e.g. age, sex, and hierarchy). In addition, several studies have highlighted the possibility that ecological factors may influence manual laterality in non-communication actions (e.g. MacNeilage et al. 1987; Hopkins et al. 2011). However, to date no study has explored the higher-level ultimate causes (i.e. evolutionary forces) of the right-handedness/left-brain specialization for language considering purely non-human primates intraspecific gestures. In particular, the extent to which intraspecific gestural laterality has

been shaped by the ecology and the sociobiology of a given species through natural selection needs to be addressed.

To contribute to this endeavour, the present study assessed and compared gestural laterality in spontaneously occurring communicative interactions between conspecifics in two great ape species, — chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*). Both species are phylogenetically very closely related to humans (e.g. Scally et al. 2012), live in relatively complex social groups (e.g. Goodall 1968; Tutin 1996) and show sophisticated gestural interactions (e.g. Call & Tomasello 2007; Pika et al. 2003). Moreover, these two species differ in their ecology and their social structure and dynamics: chimpanzees are both terrestrial and arboreal (e.g. Doran 1996) and live in multi-male–multi-female groups characterized by a highly variable party membership, whereas gorillas are mainly terrestrial (e.g. Ankel-Simons 2007) and live in polygamous and generally cohesive groups (e.g. Aureli et al. 2008; Pika 2007). Choosing such species with different ecology as well as social structure and dynamics will enable a better understanding of the possible influence of these socioecological factors on intraspecific gestural laterality.

To achieve this goal we studied three groups of chimpanzees and three groups of gorillas living in socio-ecologically relevant captivity conditions (i.e. when naturalization of enclosures is stimulating and social groups include many subjects). Such captivity conditions are ideal to study and compare non-human primates' gestural communication because 1) they allow (unlike the wild) fairly physically comparable conditions in terms of opportunities for seeing one another, traveling, climbing, and so forth (e.g. Call & Tomasello 2007), 2) growing evidence does not show a significant effect of captivity and human presence on laterality for non-communication actions (e.g. chimpanzees: Hopkins et al. 2003; Llorente et al. 2011) and gestures (e.g. chimpanzees: Hopkins et al. 2005; Fletcher 2006), and 3) they enable to consider large sample size and number of data points per individual especially required to perform reliable and more comprehensive analysis (e.g. Prieur 2015; Prieur et al. 2016a).

We addressed the following two main research questions:

(Question 1) Do chimpanzees and gorillas exhibit stable direction of laterality when producing different types of intraspecific gestures at the individual level and is this related to the strength of laterality?

To answer this question, we investigated the production of the most frequent types of gestures produced by chimpanzees and gorillas which have been reported in well-established ethograms (Nishida et al. 2010) and gesture studies (chimpanzees: e.g. Call & Tomasello

2007; gorillas: e.g. Pika et al. 2003). First, we separately assessed laterality at the individual level for 21 intraspecific gestures produced by chimpanzees and 16 produced by gorillas. Secondly, for both species we studied the possible relationships between the stability of the direction and strength of laterality in each gesture taken separately, then simultaneously considering all gestures. Based on literature showing an influence of gestural and individual sociodemographic characteristics on chimpanzees' right-hand use (e.g. Hobaiter & Byrne 2013; Prieur et al. 2016a), we predicted firstly that we would find both 'stable' and 'nonstable' lateralized individuals. In other words, the direction of laterality in 'stable' individuals would not be dependent on the type of gesture *per se* whereas in 'unstable' individuals it would be gesture-specific (prediction n°1). Secondly, we expected that stable individuals would exhibit a higher degree of laterality than nonstable individuals (prediction n°2).

(Question 2) Is there a species difference in gestural laterality at the population level (i.e. when considering all our subjects as a whole)? If yes, which factors could explain this difference?

To answer this question, we examined the most frequent gestures shared by both chimpanzees and gorillas (a total of 14 shared gestures). We compared the direction and strength of gestural laterality between both species taking into account, first, each of these gestures (considered separately), then all gestures simultaneously (i.e. considered as a whole). Next, to further our between-species comparison, we performed a multifactorial investigation taking simultaneously into account the respective influences of the following three categories of factors previously found to modulate chimpanzees' and gorillas' gestural laterality (e.g. Prieur 2015; Prieur et al. 2016a): 1) interactional context components, 2) signal characteristics and 3) signaller's socio-demographic characteristics. We predicted differences in gestural laterality between both species related to their socioecology and influenced by these three factors. More precisely, based on the postural origins theory of handedness for manipulation (MacNeilage et al. 1987, 2007), we expected to find a difference in gestural laterality between both species related to their particular degree of arboreality/terrestriality (prediction n°3). As different species are known to show differences in laterality in relation to their different social structures (e.g. Sovrano et al. 1999; Bisazza et al. 2002), we predicted that gorillas living in relatively stable social groups (with gestural interactions with the same individuals possibly taking place at higher frequencies) would be more likely to exhibit stability in laterality (in direction and/or in strength) than chimpanzees which have less stable social structures

including daily fission-fusion social dynamics and thus highly variable party memberships (prediction n°4).

2. Results

2.1. Stability of the direction of chimpanzees' and gorillas' gestural laterality

To investigate whether and how chimpanzees and gorillas exhibit stable direction of gestural laterality at the individual level (Question 1), we first quantified their individual laterality bias focusing on the most frequently produced gestures of chimpanzees (N=21) and gorillas (N=16) reported in previous studies (e.g. Nishida et al. 2010; Pika et al. 2003). We then examined the potential relationships between stability of the direction and strength of gestural laterality. Over all the subjects (39 chimpanzees and 35 gorillas) we recorded a total of 25,534 gesture occurrences for chimpanzees and a total of 16,801 for gorillas. After applying the statistical criteria required for performing the binomial test 25,024 gesture occurrences for chimpanzees and 16,471 for gorillas were retained for descriptive statistics and related analyses. The mean number of gesture occurrences per subject was 641.64 for chimpanzees (minimum=29, maximum=3 198; SD=764.16) and 470.60 for gorillas (min=6, max=1 771; SD=504.34).

2.1.1. Stability of the direction of laterality at the individual level.

Over all the subjects, we found a total of 12 chimpanzees and nine gorillas were lateralized for at least six gesture types (Appendix Table A1 and Table A2). Among the 12 chimpanzees, six exhibited stable hand preferences towards the right over gesture types (binomial test: $P \leq 0.031$; Appendix Table A1) and six did not ($P \geq 0.070$; Appendix Table A2). Among the nine gorillas, six exhibited stable hand preference towards the right over gesture types ($P \leq 0.016$; Appendix Table A3) and three did not ($P \geq 0.219$; Appendix Table A4).

2.1.2. Relationships between stability of the direction and strength of gestural laterality

Considering ABSHI values (i.e. absolute values of handedness index (HI)) of each gesture type taken separately, we showed that the six stable chimpanzees did not have a stronger laterality than the six non-stable chimpanzees for any considered gesture type (Table 4). By comparison, the six stable gorillas showed a stronger laterality than the three non-stable gorillas for two gesture types with object (n1=6, n2=3; PUT OBJECT ON HEAD/BACK: $U = 18$;

$P = 0.024$, SHAKE OBJECT: $U = 18$; $P = 0.024$) and one gesture without object ($n_1=6$, $n_2=3$; TOUCH BODY: $U = 18$; $P = 0.024$; Table 4).

Simultaneously considering all gesture types, we found that the six stable chimpanzees did not exhibit a stronger laterality than the six non-stable chimpanzees (one-sample Wilcoxon signed-rank test: $W = 154$; $P = 0.191$). By comparison, we showed that the six stable gorillas tended to exhibit a stronger laterality than the three non-stable gorillas ($W = 105$; $P = 0.058$).

In sum, stable gorilla subjects exhibited a higher strength of laterality than non-stable gorilla subjects. However, this was not true for all chimpanzees considered in this study.

2.2. Comparisons between chimpanzees' and gorillas' intraspecific gestural laterality

To assess whether there is a species difference in gestural laterality at the population level and its cause (Question 2) we assessed the 14 gestures shared by both species. First, we compared the direction and strength of gestural laterality between both species. Second, to further our between-species comparison, we used a comprehensive approach considering the influence of three categories of factors previously found to modulate gestural laterality (e.g. Prieur 2015).

2.2.1. Direction and strength of laterality

Over all the subjects, we recorded a total of 20,608 gesture occurrences for chimpanzees and a total of 14,572 for gorillas. After having applied the statistical criteria required for performing the binomial test, a total of 20,306 gesture occurrences for chimpanzees and 14,283 for gorillas were retained for descriptive statistics and related analyses. The mean number of gesture occurrences per subject was 520.67 for chimpanzees (minimum=21, maximum=2 952; $SD=660$) and 408.09 for gorillas (minimum=6, maximum=1 550; $SD=435.75$).

Taking into account each of the 14 gestures (i.e. considered separately), we showed that chimpanzees were less right-handed than gorillas for SLAP HAND (Mann-Whitney test: $U = 265$, $P = 0.026$; Table 5). On the contrary, chimpanzees were more right-handed than gorillas for THROW OBJECT ($U = 143$, $P = 0.009$) and they showed a stronger laterality than gorillas for this gesture ($U = 165$, $P = 7.79e-05$).

Simultaneously taking into account all the 14 gestures (i.e. considered as a whole), we did not find differences in both the direction and the strength of gestural laterality between

chimpanzees and gorillas (one-sample Wilcoxon signed-rank test: Mean HI: $W = 57$, $P=0.808$; Mean ABSHI: $W = 62$, $P = 0.583$).

2.2.2. Factors and their mutual interactions influencing chimpanzees' and gorillas' gestural laterality

To further our between-species comparison across all subjects, we simultaneously took into account the following three potentially influencing categories of factors and their interactions: interactional context components, gesture characteristics and individual sociodemographic characteristics. We performed a generalized linear mixed model (GLMM) analysis considering all the gesture occurrences (a total of 20,608 for chimpanzees and of 14,572 for gorillas). The mean number of gesture occurrences per subject was 528.41 for chimpanzees (minimum=28, maximum=2 953; $SD=656.48$) and 416.34 for gorillas (minimum=11, maximum=1 550; $SD=433.01$).

The analysis of deviance results corresponding to the best GLMM model are displayed in Table 6. We only considered significant interactions including the variable “Species”, which was the focus variable. The other variables/interactions introduced into our model are only present in order to adjust for any possible effect of “Species” on the dependent variable “Hand use” (see more detailed analyses and results about both chimpanzees' and gorillas' gestural laterality in Prieur 2015). The results of post-hoc multiple comparisons are displayed in Appendix Table A5. For clarity, only significant p-values of post-hoc multiple comparison tests are mentioned in the text below whereas all p-values can be found in Table A5.

Influence of species. Gorilla signallers were more right-handed than chimpanzee signallers to perform auditory gestures (Fig. 1a) (Tukey test: $P = 0.002$). This was also true when the recipient was in the left visual field of the signaller (SVF_L) (Fig.1b) ($P = 0.004$).

Influence of the position of the recipient in the signaller's visual field during interaction (SVF). Chimpanzee and gorilla signallers used their right hand more when the recipient was in their right visual field (SVF_R) than in their left visual field (SVF_L) during an interaction (Fig.1b) (Tukey test: for both species: $P < 0.0001$).

Influence of gesture sensory modality. Chimpanzee signallers were more right-handed when performing visual gestures than when performing auditory gestures (Fig.1a) (Tukey test: $P = 0.0003$) and when performing visual gestures than when performing tactile gestures (Fig.1a)

($P = 0.004$). Gorilla signallers were more right-handed when performing auditory gestures than when performing tactile gestures (Fig. 1a) ($P = 0.035$).

3. Discussion

The aim of the present study was to contribute to the investigation of the proximate and distal causes of the right-handedness/left-brain specialization for language by considering the laterality of chimpanzees' and gorillas' most frequently expressed intraspecific gestures. To do so, we addressed two main research questions. Firstly, do chimpanzees and gorillas exhibit stable direction of laterality when producing different types of gestures at the individual level and if yes is it related to the strength of their laterality? Secondly, is there a species difference in gestural laterality at the population level and if yes which factors could explain this difference? In the following paragraphs, we will present and discuss all results in detail.

3.1. Stability of the direction of chimpanzees' and gorillas' gestural laterality (Question 1)

Consistent with our first prediction we found both 'stable' and 'non-stable' lateralized individuals in both species. More precisely, we found an equal distribution of stable and non-stable chimpanzees (6 of the 12 lateralized subjects). In contrast, there was a trend concerning the distribution of stable versus non-stable gorillas (6 of the 9 lateralized subjects). A higher number of gorillas showed stability in their direction of gestural laterality while a minority were classified as non-stable, showing gesture-specificity in their direction of laterality. These findings provide evidence for the existence of stable individual hand preferences in both chimpanzees and gorillas. They are consistent with previous studies showing that hand preferences for different gesture types were significantly correlated with each other within the same individuals: for 59 chimpanzees between human-directed FOOD BEG and a category of 3 species-typical gestures directed towards both humans and conspecifics (pooled data) combining THREAT, EXTEND ARM and HAND SLAP Meguerditchian et al. 2010; for 15 baboons between human-directed FOOD BEG and HAND SLAP directed towards both humans and conspecifics (pooled data) (Meguerditchian & Vauclair 2009). Interestingly, studies have shown that in both chimpanzees (Meguerditchian et al. 2010) and baboons (Meguerditchian et al. 2011) hand preferences for particular gesture types are stable over time. Our findings showing gesture-specificity in the direction of laterality for non-stable chimpanzee and gorilla subjects are in accordance with prior studies reporting that in chimpanzees laterality can be

modulated according to the type of gesture performed (in captivity: e.g. Hopkins & Wesley 2002; Prieur et al. 2016a; in the wild: Hobaiter & Byrne 2013) and for captive gorillas (Prieur 2015; Prieur et al. submitted).

Simultaneously considering the most frequently performed gestures of all of chimpanzees and gorillas in this study we showed that stable gorillas tended to exhibit a stronger laterality than non-stable gorillas but this effect was not found in the chimpanzee dataset. Therefore, our second prediction that stable individuals would exhibit a higher degree of laterality than non-stable individuals is verified for gorillas but not for chimpanzees.

Overall, the difference of stability patterns observed between chimpanzees and gorillas at both the individual and population levels may be better explained by the particular social structure and dynamics of the two species (prediction n°4) than by their particular degree of arboreality/terrestriality (prediction n°3). We hypothesized that social cohesion among members of gorilla groups would facilitate the emergence of a certain degree of stability in their direction of gestural laterality that may have led to an increase in the strength of gestural laterality, possibly resulting in greater alignment of gestural laterality among group members. Conversely, the more flexible and fluid social grouping of chimpanzees would have facilitated a certain degree of flexibility in their direction of gestural laterality that may not have led to an increase in the strength of gestural laterality. We supposed that such flexibility would have favoured the adjustment of gestural laterality between members of different sub-groups, possibly exhibiting different laterality patterns and thus social coordination and interactions within the group.

Taking a wider evolutionary perspective into account, we postulate that both stability and flexibility in the direction of gestural laterality, at least in primates, may differently modulate the strength of gestural laterality depending on the species' social structure and dynamics. This intertwining effect between direction and strength of gestural laterality might have played a crucial role in providing advantages at both the individual and population levels: first, in improving behavioural efficiency particularly in the brain's processing of gestural communication, and second in facilitating social coordination and interactions. This may eventually have contributed to the emergence and development of a complex multimodal language and a strong bias towards right-handedness in humans.

These hypotheses are supported by many studies showing that brain and behavioural lateralization would have significantly contributed to biological fitness at both the individual and population levels (e.g. see Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Mac Neilage et al. 2009 for reviews). Further studies considering a greater number of stable

subjects and investigating not only their strength of laterality but also their communication efficiency and fitness are necessary to test these hypotheses.

3.2. Comparisons between chimpanzees' and gorillas' intraspecific gestural laterality (Question 2)

3.2.1. Direction and strength of laterality

The between-species comparison of gestural lateralities in our study showed that chimpanzees and gorillas differ from one another for two particular gestures shared by both species: SLAP HAND and THROW OBJECT. With regards to the gesture type SLAP HAND, chimpanzees were less right-handed than gorillas and their strength of laterality tended to be weaker than in gorillas. With regards to the gesture type THROW OBJECT, chimpanzees were more right-handed and showed a stronger laterality than gorillas. However, we did not find any evidence for statistical differences between the gestural laterality of both species when all 14 gestures shared by both chimpanzees and gorillas were assessed simultaneously. These findings thus raise the following issue: Why would species differences concerning gestural laterality emerge in the two particular gesture types SLAP HAND and THROW OBJECT?

Handedness appears to be multidimensional in both humans (e.g. Healey et al. 1986; Steenhuis & Bryden 1989) and non-human primates (e.g. Wesley et al. 2002; Prieur 2015). Therefore, a methodology that is not focused on the micro-level of distinct gesture types but takes into account the multifactorial aspect of gestural laterality (e.g. GLMM analysis: Prieur 2015; Prieur et al. 2016a) is a more appropriate method to perform between-species comparisons. Findings associated with our multifactorial investigation are discussed below.

3.2.2. Factors and their mutual interactions influencing chimpanzees' and gorillas' gestural laterality

A multifactorial investigation of chimpanzees' and gorillas' intraspecific gestural laterality revealed similarities (statistical non-differences) but also differences between the two species. With regards to similarities (statistical non-differences) between both species, we showed that both chimpanzee and gorilla signallers used their right hand more when the recipient was in their right visual field (SVF_R) than in their left visual field (SVF_L) during an interaction. This is consistent with our previous results for tactile and visual gestures of both chimpanzees and gorillas (Prieur 2015; Prieur et al. 2016a; Prieur et al. submitted).

However, in contrast to tactile and visual gestures, chimpanzee signallers preferentially used the contralateral hand (i.e. the hand on the side opposite to the recipient) for auditory gestures. As the 14 gestures shared by both chimpanzees and gorillas, include 6 tactile gestures, 6 visual gestures and 2 auditory gestures, tactile and visual gestures are overrepresented in our data compared to auditory gestures giving them greater weight in analyses of hand preference and this could explain our result indicating that signallers used their right hand to perform gestures more in SVF_R than in SVF_L situation.

The between-species comparison of gestural laterality showed that gorilla signallers were more right-handed than chimpanzee signallers to perform auditory gestures. This is in line with Pika and colleagues' (2005b) review showing first that visual and tactile gestures were more common than auditory gestures in chimpanzees' and gorillas' gestural repertoires. These authors also noted that auditory gestures represented a greater part (about one fifth) of gorillas' than of chimpanzees' (about one-tenth) gestural repertoire. We hypothesize that this difference may be due to the generally higher inter-individual distances kept by gorillas (Klein 1999) compared to chimpanzees (Harcourt 1979; White & Chapman 1994). These distances would make auditory signals particularly relevant for gorillas to more easily attract the attention of an audience. As auditory gestures are more common in gorillas' than in chimpanzees' repertoires, they are likely to be more codified/lateralized than for chimpanzees, possibly enabling better social coordination. Such findings suggest that gestural laterality of our close living relatives (chimpanzees and gorillas) might have been shaped by selection pressures in relation to social structure and dynamics. This is in line with our fourth prediction. Furthermore, this is consistent with recent studies showing that alignment of gestural laterality could result from different types of social pressures (chimpanzees and gorillas: Prieur 2015; Prieur et al. 2016a; Prieur et al. submitted; humans: Chapelain et al. 2015). Our findings thus provide additional support for the 'social theory of the origins of laterality' (e.g. see Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005 for reviews) postulating that social pressures have acted in determining laterality through natural selection.

In this study we showed that gorilla signallers were more right-handed than chimpanzee signallers when the recipient was in the left visual field of the signaller. Many studies investigating emotion perception of facial expressions have indicated a left visual field (right hemisphere) advantage to perceive emotions for humans (e.g. Burt & Perret 1997), non-human primates (e.g. chimpanzees and gorillas: Quaresmini et al. 2014), and phylogenetically more distant species (e.g. domestic dogs, *Canis familiaris*: Guo et al. 2009). Moreover, several studies examining the effect of emotional state (emotional valence *per se* and stress-

related emotional states) on laterality have suggested that negative emotional state would induce a right-side bias use for humans (e.g. Rohlfs & Ramirez 2006), chimpanzees and gorillas (Prieur 2015; Prieur et al. 2016a) and phylogenetically more distant species (e.g. rats, *Rattus spp.*: e.g. Castellano et al. 1989). In addition, it has been documented that gorillas seem to be much more sensitive than chimpanzees to environmental changes/stressful conditions (e.g. Zaragoza et al. 2011; Masi et al. 2012). On the basis of the above-mentioned literature, we hypothesized that gorillas may be more sensitive to negative emotional state (when perceiving the recipients' facial expression with their left visual field) than chimpanzees. This assumption might explain why gorillas exhibited greater right-hand use than chimpanzees when the recipient was in the left visual field of the signaller. Additional studies are required to test this hypothesis.

3.3. Conclusion

To conclude, our study provided the first evidence that organisms of a given species (chimpanzees and gorillas) exhibit either stability or flexibility of their hand preference with regards to the most frequently used gestures of their natural repertoire. Both stability and flexibility in the direction of gestural laterality may differently modulate the strength of laterality in relation to the species social structure and dynamics. Such a hypothesized intertwinement effect might have provided advantages at both the individual and population levels: first, in increasing individual brain efficiency, and particularly communication related-functions, and second in facilitating social coordination and interactions. By performing the first between-species comparison of intraspecific gestural laterality, our study suggests that social structure and dynamics of both chimpanzees and gorillas may have differently impacted gestural laterality in these species through the influence of gesture sensory modality and the position of the recipient in the signaller's visual field during interaction. Our study thus provides additional support to the social theory of the origins of laterality (e.g. Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005) proposing that social pressures have acted in shaping laterality through natural selection.

4. Experimental procedures

A more detailed description of all subjects and of the observational and coding procedures can be found in previous studies (Prieur 2015; Prieur et al. 2016a).

4.1. Subjects

We observed a total of 39 chimpanzees raised under semi-natural conditions in three different zoos in Europe: Leipzig Zoo, Germany ($N=16$), Beauval Zoo, France ($N=14$) and La Palmyre Zoo, France ($N=9$). The age of the 26 females and 13 males ranged from 0,7 to 54 years (Mean=20.92; SD=13.36).

In addition, we observed a total of 35 western lowland gorillas (*Gorilla gorilla gorilla*) raised under semi-natural conditions in three different zoos in Europe: La Vallée des Singes, France ($N=11$), Apenheul Primate Park, the Netherlands ($N=14$) and Burgers' Zoo, the Netherlands ($N=10$). The age of the 23 females and 12 males ranged from 0,5 to 42 years (Mean=13.64; SD=13.07).

Based on previous studies of chimpanzees (Goodall 1986) and gorillas (Breuer et al. 2009; Stoinski et al. 2013) and to enable within- and between-species comparisons, individuals were clustered into the following age categories: immatures (0–6 years old), adolescents (7–12 years old), young adults (13–20 years old), and mature adults (over 20 years old). The individuals' demographic characteristics (age, sex and zoo) and housing conditions have been described in previous work (Prieur 2015).

The six above-mentioned European zoos were chosen because they provided relatively similar favourable captivity conditions for the study chimpanzees and gorillas (naturalization of enclosures is stimulating and social groups include many subjects). The zoo enclosures and their arrangements varied, however, all outdoor enclosures offered large naturalistic environments surrounded by a water ditch and contained climbing structures (e.g. trees, ropes and platforms) as well as vegetation (e.g. bamboo and various types of bushes and grass). All indoor enclosures also included climbing structures. The enclosures in the zoos in Leipzig and La Palmyre also contained vegetation such as bushes and grass. Branches were also proposed as additional environmental enrichment for both the chimpanzees and gorillas. Zookeepers fed the study subjects three to five times a day (depending on the zoo) with a variety of fresh fruits, vegetables, branches with leaves, seeds, wood, and raisins supplemented with primate pellets, vitamins and mineral drinks. Water was available *ad libitum*. These captivity conditions ensured the welfare of all animals. Since our study was of a purely non-invasive nature involving only observations of animals in their enclosures, neither experimental permits nor ethical approvals were required.

4.2. *Observation procedure*

Observation data were collected by J.P from July to December 2013 for chimpanzees (total: 705 h observations) and from May 2012 to June 2013 for gorillas (total: 651 h observations), 6 h a day during 4 sessions of 1.5 h, two in the morning and two in the afternoon. Data were collected using the behaviour sampling rule “sampling all occurrences of some behaviours” with “continuous recording” for the recording rule (Altmann 1974; Martin & Bateson 1994). Observation data were collected in real time using a stopwatch, a paper sheet onto which data were recorded as well as powerful pair of binoculars if necessary. Data collection was mostly performed from above and as close as possible to the subjects. Data were only recorded when a clear view of the subjects was possible. We kept track of all of each individual’s daily recorded behaviours so that all subjects were observed for as similar lengths of time as possible.

4.3. *Coding procedure*

We only considered gestures produced during dyadic interactions that fulfilled the following four key criteria of intentional communication: (1) sensitivity to the recipient’s attentional state as evidenced by the adjustment of the signaller’s communication in relation to the recipient’s attention (e.g. emitting a visual signal only when the recipient is looking), (2) response waiting as evidenced by the signaller pausing (for at least two seconds) while maintaining visual contact with the recipient, (3) signaller’s apparent satisfaction (as evidenced by signaller ceasing communication) when the initial signal was successful as it achieved the social goal and (4) signaller’s goal persistence (as evidenced by repetition and/or elaboration) when the initial signal was unsuccessful as it did not achieve the social goal (e.g. Fröhlich et al. 2016). For each dyadic interaction, we recorded (1) type of gesture (Table 1, see below for further details), (2) limb (hand/foot) used by the signaller to communicate, (3) laterality (left or right hand/foot), (4) interactional context of gestural production considering the relative positions of the two subjects before and during an interaction (both visual field and body side), (5) emotional context associated with the interaction, and (6) identity and role (signaller or recipient) of both subjects, as described below.

Based on Pika and Bugnyar’s (2011) definition of gesture, only intentionally produced behaviours that met the following characteristics were classified as gestures: They (a) were used to initiate a social interaction, (b) were directed towards a recipient, (c) were

mechanically ineffective (e.g. Pollick & de Waal 2007), and (d) elicited a voluntary response by recipients.

Because only two gestures involved the foot (SLAP FOOT and KICK), we used the term ‘hand’ instead of ‘limb’ for simplicity. Which hand was used to communicate was recorded during dyadic interactions only when both hands of the signaller were free and symmetrically positioned with respect to the subject’s body midline before the interaction, without any environmental factors that could influence the use of one hand (e.g. close to a wall/bush/tree).

Data were recorded when a gesture was produced either singly or in a gesture bout (i.e. sequence of gestures separated by intervals; e.g. Marchant & McGrew 1991). Only the first gesture of a bout was recorded. The following criteria had to be met to consider that a single gesture or a bout was terminated: (1) the signaller's hand returned to its initial position (Meguerditchian et al. 2010), (2) the signaller switched to another non-communicative activity (e.g. foraging, resting), or (3) the movement was influenced by an outside incident (e.g. stumble; e.g. Harisson & Nystrom 2010). A gesture was recorded as a new gesture event when a change in hand activity lasted more than 3 seconds (e.g. the signaller ceased to communicate by leaving the location to search for food sources during more than 3s) thus ensuring statistical independence of data (e.g. Hopkins & de Waal 1995).

4.4. *Gesture characteristics*

All gesture classifications were based on descriptions of previous gestural repertoires (when necessary anatomical elements or precisions were added; Tables 1 and 2). We considered 21 different gestures for chimpanzees and 16 different gestures for gorillas. In accordance with Pika and colleagues (2003, 2005a), these gestures were divided into three communication modalities: 1) auditory gestures that generate sound while being performed, 2) visual gestures that generate a mainly visual component with no physical contact, and 3) tactile gestures that include a physical contact with the recipient. These gestures were performed either with or without an object used as a communication tool. We measured the time subjects took to perform a single gesture: the starting point was determined by a hand starting to move, the end point when the hand was again in a resting position (e.g. McNeill 1992). Gestures lasting less than 2 s were categorized as ‘short’ gestures and gestures lasting more than 2 s were categorized as ‘long’ gestures. This categorization was defined following a pilot study (Prieur 2015) so that the parameter “gesture duration” was not measured/noted during the data collection period. Gestures were also divided as follows: some gestures were

categorized as “rare”, defined as gestures performed by only a few subjects in our population (i.e. performed by 13 of the 39 chimpanzees; and by 17 of the 35 gorillas); and the other gestures were categorized as “common”, namely gestures performed by most of the subjects in the population (i.e. performed by at least 25 chimpanzees; and by at least 19 gorillas). Note that no gesture characteristic – sensory modality (auditory, visual or tactile), use of a communication tool (with or without), gesture duration (short or long) and sharing degree (rare or common) – was recorded during the data collection (on-site at the zoo). Indeed, each gesture type being associated to intrinsic characteristics, only the gesture type had to be recorded. Every gesture characteristic was taken into account (via the recorded gesture type data set) for subsequent statistical analysis.

4.5. Characteristics of the interactional context of gesture production

For each dyadic interaction, we recorded the relative positions (visual field used and exposed body side) of both subjects before (the last position for 2 s before an interaction) and during the interaction. The visual field used refers to the spatial extent (from 0 to 180°) in which the recipient is located (i.e. on the left or on the right visual field of the signaller). It was termed “enlarged field” by Baraud and colleagues (2009). Since Prieur (2015) found strong positive correlations between recorded position variables, we only considered the two following position variables: 1) the position of the recipient in the signaller’s visual field during interaction (noted SVF) and 2) the position of the signaller in the recipient’s visual field during interaction (noted RVF). Note that in very rare cases (for chimpanzees: 77 of the 25,534 occurrences of interactions/gestures recorded in total; for gorillas: 8 of the 16,801 occurrences recorded in total), the orientation of the signaller or the recipient could not be recorded.

The emotional contexts of interactions were divided into two categories, positive and negative, according to three criteria. The emotional context was inferred primarily according to (1) the functional consequences of the gesture during an interaction (the response of the recipient to the signaller's gesture), but also, if necessary, (2) the global social context in which the given interaction occurred (positive valence: affiliative, food, nurse, play, ride and travel; negative valence: agonistic; see for definitions Pika et al. 2003; Pollick & de Waal 2007), and (3) the signaller’s facial (e.g. Parr & Waller 2006; Waller & Cherry 2012) and vocal (e.g. Goodall 1986; Crockford & Boesch 2005; Salmi et al. 2013) expressions and, to a lesser extent, whole-body expressions (e.g. Schaller 1963; Van Hooff 1973) (Supplementary

Table S1 and Table S2). We classified a gesture as positive when it was, for instance, accompanied by a relaxed facial expression, a vocalization used only in affiliative contexts (e.g. ‘Aaa’ grunt for chimpanzees; single grunt for gorillas) and a global social context of an affiliative nature (e.g. feeding, resting).

4.6. Sociodemographic characteristics of the subjects

In addition to the subject’s demographic characteristics (age, sex and zoo), data concerning genetic relatedness (kin) and social relationships (affiliation and hierarchy) were considered (Prieur 2015; Prieur et al. 2016a).

4.6.1. Kinship

We were given permission to use data concerning the genetic relationships of all individuals observed. Three different categories of chimpanzee and gorilla dyads were considered: (1) ‘Parent–infant’ including mother–infant and father–infant dyads, (2) ‘siblings’ including siblings and half-siblings, and (3) ‘unrelated’ for dyads of genetically unrelated subjects.

4.6.2. Affiliation

We used the Dyadic Affiliation Index (DAI) defined by Prieur and colleagues’ (Prieur 2015; Prieur et al. 2016a) to measure relationship quality based on the relative frequencies of affiliative and agonistic behaviours within the dyad. DAI increases with affinity, starting from 0 in the absence of affinity. Three categories of dyadic affiliation were considered: (1) “Low” from 0 to 0.5 (389 dyads for chimpanzees and 335 for gorillas), (2) “Medium” from 0.5 to 1 (58 dyads for chimpanzees and 31 for gorillas) and (3) “High” more than 1 (47 dyads for chimpanzees and 36 for gorillas).

Affiliative and agonistic behaviours were selected based on previous studies in the wild (e.g. chimpanzees: Goodall 1986; Nishida et al. 2010; gorillas: Harcourt 1988; Robbins 1996, 2008) and in captivity (e.g. chimpanzees: Pollick & de Waal 2007; gorillas: Pika et al. 2003; Genty et al. 2009). We considered the following strict affiliative gestures (i.e. gestures that are expressed only in positive contexts; 8986 for chimpanzees and 4477 for gorillas) to quantify affiliation: EMBRACE, EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, EXTEND HAND (only for chimpanzees), and TOUCH BODY. All recorded agonistic interactions were considered (4334 for chimpanzees and 1039 for gorillas). These interactions include

both the mechanically ineffective gestures considered for chimpanzees and gorillas respectively and also SLAP BODY and SLAP for chimpanzees and KICK and SLAP for gorillas (Pika et al. 2003) that did not meet the statistical criteria required for performing binomial tests (see details below in Descriptive statistics). Two mechanically effective manual actions directed towards a social partner for both chimpanzees and gorillas were also included: GRAB and PUSH (Pika et al. 2005a; variants with sufficient force to move recipient's body).

4.6.3. *Hierarchy*

We evaluated hierarchical dominance relationships on the basis of agonistic interactions (e.g. Pollick & de Waal 2007; Robbins 2008) when the aggressor and the recipient of a threat were clearly identified (e.g. Lehner 1996; Langbein & Puppe 2004). All recorded agonistic interactions (4334 for chimpanzees and 1039 for gorillas) were considered. These interactions were organised into socio-metric matrices and analyzed using the program MatMan 1.1 (Noldus Information Technology, Wageningen, Netherlands; de Vries 1995, 1998; de Vries et al. 2006). MatMan 1.1 assigns a rank from 1 (the most dominant) to N (the most subordinate) to each of the N subjects of one zoo. We considered the following three categories of hierarchical rank 'Subordinate', 'Intermediate' and 'Dominant' for chimpanzees (Beauval group: five subordinates, five intermediates and four dominants; Leipzig group: five subordinates, five intermediates and six dominants; Palmyre group: three subordinates, three intermediates and three dominants) and for gorillas (Apenheul: 7 subordinates, 3 intermediates and 4 dominants; Burgers: 4 subordinates, 4 intermediates and 2 dominants; La Vallée: 6 subordinates, 2 intermediates and 3 dominants).

4.7. *Statistical analysis*

All statistical analyses were computed using R version 3.0.3 (R Development Core Team 2014). The level of significance was set at 0.05.

4.7.1. *Descriptive statistics of laterality at the individual and population levels*

To enable subsequent statistical analyses (binominal test), we only considered data of those gesture types that had been recorded at least six times being performed by at least six different chimpanzee subjects and six different gorilla subjects (Chapelain 2010; Prieur et al. 2016a).

Binomial tests on the numbers of responses performed with the left and right hands assessed individual-level biases for each of the most frequent gestures (21 for chimpanzees

and 16 for gorillas). A subject presenting a significant bias (respectively no bias) was categorised as lateralized (respectively non-lateralized). Only considering lateralized subjects (biased towards the right or the left) for at least six gestures, we then performed binomial tests to evaluate the significance of differences between the numbers of left and right lateralized gestures for each subject (i.e. to evaluate the subject's stability of the direction of laterality over the most frequent gestures). A subject presenting either a significant bias or no bias was categorised as either a stable or a nonstable individual respectively. For comparison purpose, we exceptionally considered one gorilla subject being significantly lateralized only for five gestures but showing two tendencies, close to significance, to be lateralized for two gestures (binomial tests: EMBRACE LATERAL: $P=0.0525$; TOUCH BODY: $P=0.0533$).

The direction of gestural asymmetry was evaluated for each subject by calculating an individual Handedness Index ($HI = (R-L)/(R+L)$, where R and L represent the total number of right- and left-hand responses respectively, and the strength of gestural asymmetry was estimated for each subject by the absolute value of HI (ABSHI) (e.g. Harris & Carlson 1993). Considering laterality on a continuum rather than dichotomously is particularly relevant to investigate more subtle relationships between handedness and cerebral lateralization (e.g. Bourne 2008). To do so and to enable comparisons with recent studies, (e.g. McGrew & Marchant 1997; Hopkins et al. 2012; Prieur et al. 2016a), we considered laterality on a continuum in order to perform both within- and between-species comparisons. Firstly, we studied relationships between stability of the direction of laterality and strength of laterality. We compared strength of laterality between stable and nonstable subjects within both species considering each of their most frequent gestures taken separately using Mann-Whitney tests, and then simultaneously, using one-sample Wilcoxon signed-rank tests which takes into account a correction for multiple comparisons. Secondly, we compared gestural laterality (direction and strength) between chimpanzees and gorillas considering each of the 14 gestures shared by both species taken separately using Mann-Whitney tests, and then simultaneously considering all these 14 gestures using one-sample Wilcoxon signed-rank tests. Thirdly, we designed and applied a multifactorial approach to more deeply investigate between-species comparisons. This analysis procedure is described below.

4.7.2. Generalized linear mixed model analysis on the multiple influential factors

To assess the effect of multiple variables on the gestural laterality of chimpanzees and gorillas we used a generalized linear mixed model (GLMM: e.g. Baayen 2008) for binary data (logistic regression) with hand use as the dependent variable based on the 14 gestures

shared by both species (Table 2). This GLMM analysis allowed the evaluation of the effects of interactional context as well as gesture and individual sociodemographic characteristics on hand use (see Table 3 for a descriptive summary of dependent, fixed and random variables). We checked every result provided by the GLMM analysis to detect potential outlier in the estimate (difference between Least Square means (LSmeans)), the standard error of the difference, the z.ratio (ratio of the estimate to its standard error) (Appendix Tables A5). All possible interactions between fixed variables were included at the beginning of the iterative model selection. Signallers' and recipients' identities were considered as the random variables to avoid pseudoreplication caused by repeated observations (Waller et al. 2013).

For the GLMM analysis, we used the 'glmer' function ('lme4' package, Bates et al. 2014) and selected the best model as the one with the lowest Akaike's information criterion (AIC). We visually checked equivariance, independence and normality of model residuals using the 'plotresid' function ('RVAideMemoire' package, Hervé 2014). The main effects of the best model were tested with type II Wald chi-square tests using the 'Anova' function ('car' package, Fox & Weisberg 2011). LSmeans and associated adjusted probabilities of right-hand use were computed using the 'lsmeans' function ('lsmeans' package, Lenth 2014). Post hoc multiple comparisons tests were performed using Tukey's honest significant difference (HSD) test (below, referred to as 'Tukey test') to prevent Type I errors and calculated between LSmeans ('lsmeans' package).

Acknowledgments

We are very grateful to all the keepers, collaborators and researchers of the Wolfgang Köhler Primate Research Center at Zoo Leipzig (Germany), the Zooparc de Beauval, the zoo of La Palmyre, the zoo of La Vallée des Singes (France), the zoo of Apenheul and the Burgers' zoo (Netherlands). We are indebted to D. Hanus, J. Call, A. Desmoulins, R. Potier, F. Perroux, T. Petit, J.-P. Guéry, F. Rietkerk, and W. Schoo for allowing us to study the chimpanzee and gorilla groups at the respective zoos and their friendliness and helpfulness. We thank A. Chapelain for advice concerning the design of the observation protocol, R. Lenth and M. Hervé for statistical advice concerning the use of "lme4" and "lsmeans" packages as well as S. Hardman for correcting the English. Moreover, we thank the editor and the reviewers for their helpful comments to improve the manuscript.

Funding

This study has been performed in the framework of a PhD funded by the French Ministry of Research and Technology with additional financial support of Rennes Metropole and the VAS Doctoral School. In addition, it was supported by a Sofja Kovalevskaja-Award of the Humboldt Foundation to S. P.

References

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227-267.
- Ankel-Simons, F. (2007). *Primate Anatomy: An Introduction*. San Diego, CA: Academic Press.
- Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., ... & Van Schaik, C. P. (2008). Fission-fusion dynamics. *Current Anthropology*, *49*(4), 627-654.
- Arbib, M. A., Liebal, K., Pika, S., Corballis, M. C., Knight, C., Leavens, D. A., ... & Pika, S. (2008). Primate vocalization, gesture, and the evolution of human language. *Current anthropology*, *49*(6), 1053-1076.
- Baayen, R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R*. Cambridge: Cambridge University Press.
- Baraud, I., Buytet, B., Bec, P., & Blois-Heulin, C. (2009). Social laterality and 'transversality' in two species of mangabeys: influence of rank and implication for hemispheric specialization. *Behavioural brain research*, *198*(2), 449-458.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version, 1(7) <http://CRAN.R-project.org/package=lme4>.
- Bennett, C., & Fried, J. (1991). Dallas Zoo-gorilla ethology study. *Gorilla Behavior Advisory Group, compilers. Compilation of gorilla ethograms*. Atlanta: Atlanta/Fulton County Zoo. p 7-24.
- Bisazza, A., De Santi, A., Bonso, S., & Sovrano, V. A. (2002) Frogs and toads in front of a mirror: lateralisation of response to social stimuli in tadpoles of five anuran species. *Behavioural Brain Research* *134*(1):417-424.

- Bourne, V. J. (2008). Examining the relationship between degree of handedness and degree of cerebral lateralization for processing facial emotion. *Neuropsychology*, 22(3), 350.
- Bowen, R. A. (1980). The behaviour of three hand-reared lowland gorillas, *Gorilla g. gorilla* with emphasis on the response to a change in accommodation. *Dodo: Journal of the Jersey Wildlife Preservation Trust*.
- Breuer, T., Hockemba, M. B. N., Olejniczak, C., Parnell, R. J., & Stokes, E. J. (2009). Physical maturation, life-history classes and age estimates of free-ranging western gorillas—Insights from Mbeli Bai, Republic of Congo. *American Journal of Primatology*, 71(2), 106-119.
- Breuer, T., Robbins, A. M., & Robbins, M. M. (2016). Sexual coercion and courtship by male western gorillas. *Primates*, 57(1), 29-38.
- Broca, P. (1865) Sur le siège de la faculté du langage articulé. *Bulletin de la Société d'anthropologie*, 6 :337-93.
- Burt, D. M., & Perrett, D. I. (1997). Perceptual asymmetries in judgements of facial attractiveness, age, gender, speech and expression. *Neuropsychologia*, 35(5), 685-693.
- Call, J., & Tomasello, M. (2007). *The gestural communication of apes and monkeys*. Mahwah, New Jersey: Psychology press.
- Castellano, M. A., Diaz-Palarea, M. D., Barroso, J., & Rodriguez, M. (1989). Behavioral lateralization in rats and dopaminergic system: Individual and population laterality. *Behavioral Neuroscience*, 103(1), 46–53.
- Chapelain, A. (2010). Hand preferences in bonobos (*Pan paniscus*) for a variety of actions: spontaneous daily actions (non-social and social), bimanual coordination (“tube task”), tool-use (“termite fishing”) and induced gestures (“begging”). Doctorate thesis, Loughborough University, UK.

- Chapelain, A., Pimbert, P., Aube, L., Perrocheau, O., Debunne, G., Bellido, A., & Blois-Heulin, C. (2015). Can Population-Level Laterality Stem from Social Pressures? Evidence from Cheek Kissing in Humans. *PloS one*, *10*(8), e0124477.
- Crockford, C., & Boesch, C. (2005). Call combinations in wild chimpanzees, *Behaviour*, *142*, 397-421.
- Doran, D. M. (1996). Comparative positional behavior of the African apes. *Great ape societies*, 213-224.
- Dubois, T., Mead, J., & Cox, C. 1991. Lowland gorillas: ethogram (Los Angeles Zoo). *Gorilla Behavior Advisory Group, compilers. Compilation of gorilla ethograms. Atlanta: Atlanta/Fulton County Zoo*, p 27–36.
- Fama, R., Sullivan, E. V., Shear, P. K., Cahn-Weiner, D. A., Marsh, L., Lim, K. O., ... & Pfefferbaum, A. (2000). Structural brain correlates of verbal and nonverbal fluency measures in Alzheimer's disease. *Neuropsychology*, *14*(1), 29.
- Fletcher, A. W. (2006). Clapping in chimpanzees: evidence of exclusive hand preference in a spontaneous, bimanual gesture. *American Journal of Primatology*, *68*(11), 1081-1088.
- Fossey, D. (1972). Vocalizations of the mountain gorilla (*Gorilla gorilla beringei*). *Animal Behaviour*, *20*(1), 36-53.
- Fossey, D. 1983. *Gorillas in the mist*. London: Hodder and Stoughton.
- Fox, J., & Weisberg, S. (2011). *An {R} companion to applied regression* (2nd ed.). Thousand Oaks, CA: Sage <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
- Fröhlich, M., Kuchenbuch, P., Müller, G., Fruth, B., Furuichi, T., Wittig, R. M., & Pika, S. (2016). Unpeeling the layers of language: Bonobos and chimpanzees engage in cooperative turn-taking sequences. *Scientific reports*, *6*.
- Gentilucci, M., & Corballis, M. C. (2006). From manual gesture to speech: a gradual transition. *Neuroscience & Biobehavioral Reviews*, *30*(7), 949-960.

- Genty, E., Clay, Z., Hobaiter, C., & Zuberbühler, K. (2014). Multi-modal use of a socially directed call in bonobos. *PloS one*, 9(1).
- Ghirlanda, S., & Vallortigara, G. (2004). The evolution of brain lateralization: A game-theoretical analysis of population structure. *Proceedings of the Royal Society of London*, 271(1541), 853-857.
- Gold, K.C. (1991). Gorilla development study. *Gorilla Behavior Advisory Group, compilers. Compilation of gorilla ethograms. Atlanta: Atlanta/Fulton County Zoo.* p 52–53.
- Goodall, J. (1968). *The behaviour of free-living chimpanzees in the Gombe Stream Reserve* (Vol. 1). Baillière, Tindall & Cassell.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns in adaptation*. Cambridge: Harvard University Press.
- Goodall, J. (1989). *Glossary of Chimpanzee Behaviors*. Tucson: Jane Goodall Institute.
- Gotts, S. J., Jo, H. J., Wallace, G. L., Saad, Z. S., Cox, R. W., & Martin, A. (2013). Two distinct forms of functional lateralization in the human brain. *Proceedings of the National Academy of Sciences of the United States of America*, 110(36), E3435–E3444.
- Guo, K., Meints, K., Hall, C., Hall, S., & Mills, D. (2009). Left gaze bias in humans, rhesus monkeys and domestic dogs. *Animal cognition*, 12(3), 409-418.
- Häberling, I. S., & Corballis, M. C. (2016). Cerebellar asymmetry, cortical asymmetry and handedness: Two independent networks. *Laterality: Asymmetries of Body, Brain and Cognition*, 21(4-6), 397-414.
- Harcourt, A. H. (1979). Social relationships between adult male and female mountain gorillas in the wild. *Animal Behaviour*, 27, 325-342.

- Harcourt, A. H., Stewart, K. J., & Hauser, M. (1993). Functions of wild gorilla close calls. I. Repertoire, context, and interspecific comparison. *Behaviour*, *124*(1), 89-122.
- Harcourt, A. H., & Stewart, K. J. (2007). *Gorilla society: conflict, compromise, and cooperation between the sexes*. Chicago: University of Chicago Press.
- Harris, L. J., & Carlson, D. F. (1993). Hand preference for visually-guided reaching in human infants and adults. In *Primate laterality* (pp. 285-305). Springer New York.
- Harrison, R. M., & Nystrom, P. (2010). Handedness in captive gorillas (*Gorilla gorilla*). *Primates*, *51*, 251–261.
- Healey, J. M., Liederman, J., & Geschwind, N. (1986). Handedness is not a unidimensional trait. *Cortex*, *22*(1), 33-53
- Hervé, M. (2014). RVAideMemoire: Diverse basic statistical and graphical functions. R package version 0.9-40 <http://CRAN.R-project.org/package=RVAideMemoire>.
- Hobaiter, C., & Byrne, R. W. (2013). Laterality in the gestural communication of wild chimpanzees. *Annals of the New York Academy of Sciences*, *1288*(1), 9-16.
- Hohmann, G., & Fruth, B. (2003a). Culture in bonobos? Between-species and with-species variation in behavior. *Current Anthropology*, *44*, 563–571.
- Hohmann, G., & Fruth, B. (2003b). Intra- and intersexual aggression by bonobos in the context of mating. *Behaviour*, *140*, 1389–1413.
- Hopkins, W. D., & de Waal, F. B. M. (1995). Behavioral laterality in captive bonobos (*Pan paniscus*): replication and extension. *International Journal of Primatology*, *16*, 261-276.
- Hopkins, W. D., & Wesley, M. J. (2002). Gestural communication in chimpanzees (*Pan troglodytes*): The influence of experimenter position on gesture type and hand preference. *Laterality*, *7*(1), 19-30.

- Hopkins, W. D., Russell, J. L., Cantalupo, C., Freeman, H., & Schapiro, S. J. (2005b). Factors Influencing the Prevalence and Handedness for Throwing in Captive Chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 119 (4), 363-370.
- Hopkins, W. D., Phillips, K. A., Bania, A., Calcutt, S. E., Gardner, M., Russell, J., ... & Schapiro, S. J. (2011). Hand preferences for coordinated bimanual actions in 777 great apes: implications for the evolution of handedness in hominins. *Journal of human evolution*, 60(5), 605-611.
- Hopkins, W. D., Pika, S., Liebal, K., Bania, A., Meguerditchian, A., Gardner, M., & Schapiro, S. J. (2012). Handedness for manual gestures in great apes. *Developments in primate gesture research*, 6, 93-111.
- Kano, T. (1992). *The last ape: pygmy chimpanzee behavior and ecology*. Stanford, CA: Stanford University Press.
- Kano, T. (1998). A preliminary glossary of bonobo behaviors at Wamba. In T. Nishida (Ed.), *Comparative study of the behavior of the genus Pan by compiling video ethogram* (pp. 39–81). Kyoto: Nissho Printer.
- Klein, (1999). *Die Sozialen Strukturen dreier Menschenarten im Jahr 2000*. Master thesis. Westfälische Wilhelms Universität, Münster, Germany.
- Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., et al. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain*, 123, 2512–2518.
- Langbein, J., & Puppe, B. (2004). Analysing dominance relationships by sociometric methods—a plea for a more standardised and precise approach in farm animals. *Applied Animal Behaviour Science*, 87, 293-315.
- Lehner, P.N. (1996). *Handbook of Ethological Methods*. 2nd ed. Cambridge University Press, Cambridge.
- Lenth, R. V. (2014). lsmeans: Least-squares means. R package version 2.11 <http://CRAN.R-project.org/package=lsmeans>.

- Luef, E. M., & Pika, S. (2014). Acoustical Variation and Contextual Specificity of a Gorilla Vocalization: A Case Study. *Psychology and Behavioral Sciences*, 3(6), 192-196.
- Luef, E. M., Breuer, T., & Pika, S. (2016). Food-Associated Calling in Gorillas (*Gorilla g. gorilla*) in the Wild. *PloS one*, 11(2), e0144197.
- MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences*, 10(02), 247-263.
- MacNeilage, P. F. (2007). Present status of the postural origins theory. *Special Topics in Primatology*, 5, 58-91.
- MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Origins of the left & right brain. *Scientific American*, 301(1), 60-67.
- Marchant, L. F., & McGrew, W. C. (1991). Laterality of function in apes: a meta-analysis of methods. *Journal of Human Evolution*, 21, 425-438.
- Martin, P., & Bateson, P. (1994). *Measuring behaviour: an introductory guide*. 2nd Ed. Cambridge: Cambridge University Press.
- Masi, S., Chauffour, S., Bain, O., Todd, A., Guillot, J., & Krief, S. (2012). Seasonal effects on great ape health: a case study of wild chimpanzees and western gorillas. *PloS one*, 7(12), e49805.
- McGrew, W. C., & Marchant, L. F. (1997). On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology*, 40, 201-232.
- McNeill, D. (1992). *Hand and Mind: What Gestures Reveal About Thought*. Chicago: University of Chicago Press.

- Meguerditchian, A., & Vauclair, J. (2009). Contrast of hand preferences between communicative gestures and non-communicative actions in baboons: Implications for the origins of hemispheric specialization for language. *Brain and Language*, *108*(3), 167.
- Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2010). Captive chimpanzees use their right hand to communicate with each other, Implications for the origin of the cerebral substrate for language. *Cortex*, *46*(1), 40-48.
- Meguerditchian, A., Molesti, S., & Vauclair, J. (2011). Right-handedness predominance in 162 baboons (*Papio anubis*) for gestural communication: consistency across time and groups. *Behavioral Neuroscience*, *125*(4), 653-660.
- Meguerditchian, A., & Vauclair, J. (2014). Communicative Signaling, Lateralization and Brain Substrate in Nonhuman Primates: Toward a Gestural or a Multimodal Origin of Language?. *Humana Mente. Journal of Philosophical Studies*, *27*, 135-160.
- Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2013). On the origins of human handedness and language: A comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. *Developmental Psychobiology*, *55*, 637–650.
- Nishida, T., Zamma, K., Matsusaka, T., Inaba, A., & McGrew, W. C. (Eds.) (2010). *Chimpanzee behavior in the wild: an audio-visual encyclopedia*. Tokyo: Springer.
- Ocklenburg, S., & Güntürkün, O. (2012). Hemispheric asymmetries: the comparative view. *Frontiers in psychology*, *3*, 5.
- Palagi, E., Antonacci, D., & Cordoni, G. (2007). Fine-tuning of social play in juvenile lowland gorillas (*gorilla gorilla gorilla*). *Developmental Psychobiology*, *49*(4), 433-445.
- Parnell, R. J. (2002). *The social structure and behaviour of western lowland gorillas (Gorilla gorilla gorilla) at Mbeli Bai, Republic of Congo* (doctorate thesis), Stirling, U.K.: University of Stirling.

- Parr, L. A., Cohen, M., & De Waal, F. (2005). Influence of social context on the use of blended and graded facial displays in chimpanzees. *International Journal of Primatology*, 26(1), 73-103.
- Parr, L. A., & Waller, B. M. (2006). Understanding chimpanzee facial expression: insights into the evolution of communication. *Social Cognitive and Affective Neuroscience*, 1(3), 221-228.
- Parr, L. A., Waller, B. M., Vick, S. J., & Bard, K. A. (2007). Classifying chimpanzee facial expressions using muscle action. *Emotion*, 7(1), 172.
- Parr, L. A., Waller, B. M., & Heintz, M. (2008). Facial expression categorization by chimpanzees using standardized stimuli. *Emotion*, 8(2), 216.
- Peirce, J. W., Leigh, A. E., & Kendrick, K. M. (2000). Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. *Neuropsychologia*, 38(4), 475-483.
- Pika, S. (2007). Gestures in subadult gorillas (*Gorilla gorilla*). In: *The Gestural Communication of Monkeys and Apes* (Ed. by J. Call & M. Tomasello), pp. 99-130. Mahwah, New York: Lawrence Erlbaum Associates.
- Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning, and use. *American Journal of Primatology*, 60, 95-111.
- Pika, S., Liebal, K., & Tomasello, M. (2005a). Gestural communication in subadult bonobos (*Pan paniscus*): repertoire and use. *American Journal of Primatology*, 65, 39-61.
- Pika, S., Liebal, K., Call, J., & Tomasello, M. (2005b). Gestural communication of apes. *Gesture*, 5(1-2), 41-56.
- Pika, S. (2012). The case of referential gestural signaling: Where next?. *Communicative & integrative biology*, 5(6), 578-582.
- Pika, S., & Bugnyar, T. (2011) The use of referential gestures in ravens (*Corvus corax*) in the wild. *Nature communications* 2:560.

- Pirmoradi, M., Jemel, B., Gallagher, A., Tremblay, J., D'Hondt, F., Nguyen, D. K., ... & Lassonde, M. (2016). Verbal memory and verbal fluency tasks used for language localization and lateralization during magnetoencephalography. *Epilepsy research*, *119*, 1-9.
- Plooij, F. X. (1984). *The behavioral development of free-living chimpanzee babies and infants*. Norwood, NJ: Ablex.
- Pollick, A. S., & de Waal, F. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 8184–8189.
- Prieur, J. (2015). *Chimpanzees' and gorillas' intraspecific gestural laterality: A multifactorial investigation* (doctorate thesis), Rennes, France: University of Rennes 1 www.theses.fr/en/2015REN1S056.
- Prieur, J., Pika S., Barbu, S., & Blois-Heulin, C. (2016a). A multifactorial investigation of captive chimpanzees' intraspecific gestural laterality. *Animal Behaviour*, *116*, 31-43.
- Prieur, J., Pika, S., Barbu, S., & Blois-Heulin, C. (2016b). Gorillas are right-handed for their most frequent intraspecific gestures. *Animal Behaviour*, *118*, 165-170.
- Prieur J., Pika S., Barbu S., & Blois-Heulin C. submitted. A multifactorial investigation of captive gorillas' intraspecific gestural laterality.
- Quaresmini, C., Forrester, G. S., Spiezio, C., & Vallortigara, G. (2014). Social environment elicits lateralized behaviors in gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *128*(3), 276.
- R Development Core Team. (2014). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org>.
- Robbins, M. M. (2008). Feeding competition and agonistic relationships among Bwindi Gorilla *beringei*. *International Journal of Primatology*, *29*(4), 999-1018.

- Rohlf, P., & Ramirez, J. M. (2006). Aggression and brain asymmetries: a theoretical overview. *Aggression and Violent Behavior, 11*, 283-297.
- Roth, R. R. (1995). *A study of gestural communication during sexual behavior in bonobo (Pan paniscus, Schwartz)*, pp. 1–119. Calgary: University of Calgary Press.
- Salmi, R., Hammerschmidt, K., & Doran-Sheehy, D. M. (2013). Western gorilla vocal repertoire and contextual use of vocalizations. *Ethology, 119*(10), 831-847.
- Scally, A., Dutheil, J. Y., Hillier, L. W., Jordan, G. E., Goodhead, I., Herrero, J. et al. (2012). Insights into hominid evolution from the gorilla genome sequence. *Nature, 483*, 169–175.
- Schaller, G. B. (1963). *The Mountain Gorilla: Ecology and Behavior*. Chicago: University of Chicago Press.
- Schaller, G.B. (1964). *The year of the gorillas*. Chicago: University of Chicago Press.
- Seyfarth, R. M., Cheney, D. L., Harcourt, A. H., & Stewart, K. J. (1994). The acoustic features of gorilla double grunts and their relation to behavior. *American Journal of Primatology, 33*(1), 31-50.
- Siebert, E. R., & Parr, L. A. (2003). A structural and contextual analysis of chimpanzee screams. *Annals of the New York Academy of Sciences, 1000*(1), 104-109.
- Slocombe, K. E., & Zuberbühler, K. (2005). Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *Journal of Comparative Psychology, 119*(1), 67.
- Sovrano, V. A., Rainoldi, C., Bisazza, A., & Vallortigara, G. (1999). Roots of brain specializations: Preferential left-eye use during mirror-image inspection in five species of teleost fish. *Behavioural Brain Research, 106* (1-2), 175-180.
- Steenhuis, R. E., & Bryden, M. P. (1989). Different dimensions of hand preference that relate to skilled and unskilled activities. *Cortex, 25*, 289-304.

- Stoinski, T. S., Perdue, B., Breuer, T., & Hoff, M. P. (2013). Variability in the developmental life history of the genus Gorilla. *American journal of physical anthropology*, 152(2), 165-172.
- Tanner, J. E., & Byrne, R. W. (1993). Concealing facial evidence of mood: Perspective-taking in a captive gorilla?. *Primates*, 34(4), 451-457.
- Tutin, C. E. (1996). Ranging and social structure of lowland gorillas in the Lope Reserve, Gabon. In W. C. McGrew, L. F. Marchant, & T. Nishida, (Eds.), *Great ape societies* (pp. 58–70). Cambridge: Cambridge University Press.
- Van Hooff, J.A.R.A.M. (1967). *The facial displays of the catarrhine monkeys and apes*. In D. Morris (Ed.), *Primate ethology* (pp.7-68). Chicago: Aldine
- Van Hooff, J. A. R. A. M. (1973). A structural analysis of the social behaviour of a semi-captive group of chimpanzees. *Social communication and movement: Studies of interaction and expression in man and chimpanzee*, 75-162.
- Vallortigara, G., & Bisazza, A. (2002) How ancient is brain lateralization. *Comparative vertebrate lateralization* 9-69.
- Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, 28, 575-589.
- de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, 50, 1375-1389.
- de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*, 55, 827-843.
- de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, 71, 585-592.

- de Waal, F. B. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behaviour*, *106*(3), 183-251.
- Waller, B. M., & Dunbar, R. I. (2005). Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (*Pan troglodytes*). *Ethology*, *111*(2), 129-142.
- Waller, B. M., & Cherry, L. (2012). Facilitating play through communication: significance of teeth exposure in the gorilla play face. *American journal of primatology*, *74*(2), 157-164.
- Waller, B. M., Warmelink, L., Liebal, K., Micheletta, J. & Slocombe, K. E. (2013). Pseudoreplication: a widespread problem in primate communication research. *Animal Behaviour*, *86*(2), 483-488.
- Wallez, C., Schaeffer, J. A., Meguerditchian, A., Vauclair, J., Schapiro, S. J., & Hopkins, W. D. (2012). Contrast of hemispheric lateralization for oro-facial movements between learned attention-getting sounds and species-typical vocalizations in chimpanzees: Extension in a second colony. *Brain and Language*, *123*, 75-79.
- Watts, D. P. (1995). Post-conflict Social Events in Wild Mountain Gorillas (Mammalia, Hominoidea). I. Social Interactions between Opponents. *Ethology*, *100*(2), 139-157.
- Wesley, M. J., Fernandez-Carriba, S., Hostetter, A., Pilcher, D., Poss, S., & Hopkins, W. D. (2002). Factor analysis of multiple measures of hand use in captive chimpanzees: an alternative approach to the assessment of handedness in nonhuman primates. *International Journal of Primatology*, *23*(6), 1155-1168.
- White, F. J., & Chapman, C. A. (1994). Contrasting chimpanzees and bonobos: nearest neighbor distances and choices. *Folia Primatologica*, *63*(4), 181-191.
- Wilke, M., Lidzba, K., Staudt, M., Buchenau, K., Grodd, W., & Krägeloh-Mann, I. (2006). An fMRI task battery for assessing hemispheric language dominance in children. *Neuroimage*, *32*(1), 400-410.

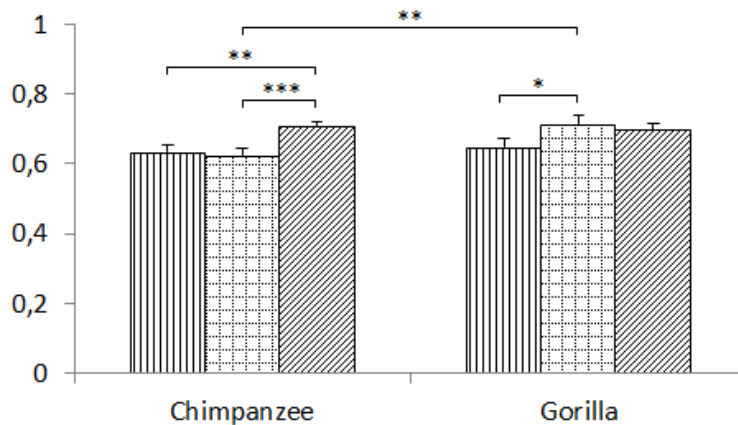
Wilke, M., Pieper, T., Lindner, K., Dushe, T., Holthausen, H., & Krägeloh-Mann, I. (2010). Why one task is not enough: functional MRI for atypical language organization in two children. *European journal of paediatric neurology*, *14*(6), 474-478.

Zaragoza, F., Ibáñez, M., Mas, B., Laiglesia, S., & Anzola, B. (2011). Influence of environmental enrichment in captive chimpanzees (*Pan troglodytes* spp.) and gorillas (*Gorilla gorilla gorilla*): behavior and faecal cortisol levels. *Revista Científica*, *21*(5), 447-456.

ACCEPTED MANUSCRIPT

Figure 1

a)



b)

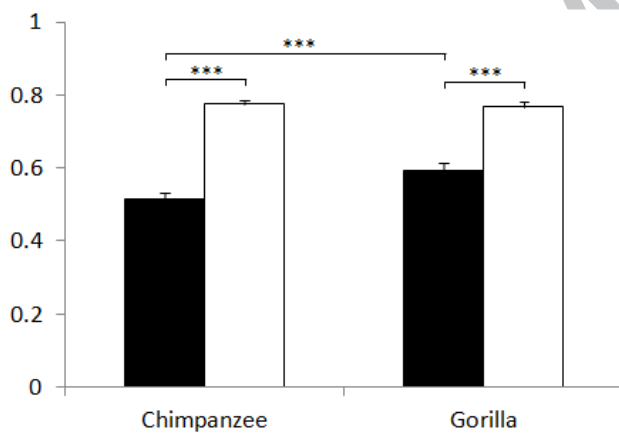


Figure 1: Adjusted probability (\pm SE) of right-hand use for each species. (a) Interactions with sensory modality: tactile, auditory, or visual gestures. (b) Interactions with Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field. Vertically striped bars: tactile gestures. Squared bars: auditory gestures. Diagonally striped bars: visual gestures. Black bars: SVF_L. Open bars: SVF_R. Tukey tests: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 1. Gestural repertoire of both chimpanzees and gorillas

| Gesture | Description | References |
|---------------------------|--|-----------------------------|
| BEAT BODY (g) | Subject slaps once or repetitively (only the hand that slapped first is considered) own body part (except chest) with knuckles or palm of hand | Pika et al. (2003, 2005a) |
| BEAT CHEST (g) | Subject slaps own chest repetitively alternating open hands or knuckles (the hand that slapped first is considered) | Pika et al. (2003, 2005a) |
| CLAP HAND * | One open hand (more often the one in the upper position) strikes against the other hand | Pika et al. (2003, 2005a) |
| SLAP FOOT * (c) | Subject hits ground/wall/object with the sole or heel of one foot | Pika et al. (2003, 2005a) |
| SLAP HAND * | Subject hits ground/wall/object with the palm of one hand | Pika et al. (2003, 2005a) |
| EMBRACE | One arm of signaller is stretched and raised up to about head level with palm facing downwards or placed lightly on the recipient's body | Roth (1995) |
| EMBRACE HALF | Subject puts one arm around another subject while walking | de Waal (1988) |
| EMBRACE LATERAL * | Subject places one arm gently around the other's shoulder, back, or waist, or puts both arms around the other while pulling the recipient closer; both partners are initially side by side and facing the same direction | Nishida et al. (1999, 2010) |
| EMBRACE VENTRAL/DORSAL * | Both arms are opened and the partner is hugged ventro/dorso-ventrally (leading arm recorded), with belly contact | de Waal (1988) |
| HAND ON (c) | The palm of one hand is placed on the head of another subject and stays there >2 sec | Pika et al. (2003, 2005a) |
| HIT WITH OBJECT * (c) | Subject clubs another subject with object (e.g. branch) held in one hand | Nishida et al. (1999, 2010) |
| KICK * (c) | Any sort of contact made with the sole/heel or fingers of one foot with another subject, without appreciable force, but the actual contact is more forceful than a simple laying of foot on another's body | Pollick & de Waal (2007) |
| PUNCH * | Any sort of contact made with fist/wrist or fingers of one hand with another subject, without appreciable force, but the actual contact is more forceful than a simple laying of the hand on another's body | Pollick & de Waal (2007) |
| PUSH (c) | Gentle pressure applied against another subject with one hand or arm | Genty et al. (2014) |
| TOUCH BODY * | Gentle and brief (<5 sec) contact of the recipient's body (except genitals) with one hand or arm | Pika et al. (2003, 2005a) |
| TOUCH GENITAL * (c) | Gentle and brief (<5 sec) contact of the recipient's genital with flat hands | Pika et al. (2003, 2005a) |
| ATTEMPT TO REACH * | Subject briefly extends hand (with fingers slightly flexed with palm up or down) towards another subject, as an attempt to touch/catch it | Pika et al. (2003, 2005a) |
| DRAG OBJECT | Subject pulls an object (e.g. branch) on the ground with one hand towards another subject | Nishida et al. (1999, 2010) |
| EXTEND HAND * (c) | Subject outstretches one hand or arm (wrist and/or fingers extended with palm up or down) towards another subject; hand or arm remains stationary | Goodall (1989) |
| PUT OBJECT ON HEAD/BACK * | Subject places an object (e.g. branch) on its head/back with one hand | Nishida et al. (2010) |
| RAISE ARM | Subject lifts one out-stretched arm (all or only forearm) overhead in a quick jerky movement with fingers slightly flexed | Plooiij (1984) |
| SHAKE OBJECT * | An object (e.g. branch) is moved back and forth with quick jerky movements of one arm, slightly or vigorously, while the subject is sitting or standing | Kano (1992, 1998) |
| THROW OBJECT * | Subject sends an object (e.g. branch) through the air with one hand towards another subject | Hohmann & Fruth (2003a, b) |

Gestures marked with (c) are considered only for chimpanzees; those marked with (g) are considered only for gorillas. Gestures are regrouped by sensory modality (for chimpanzees: 3 auditory, 11 tactile and 7 visual gestures; for gorillas: 4 auditory, 6 tactile and 6 visual gestures) and presented by alphabetic order. Gestures marked with * are followed by descriptions inspired from the mentioned reference(s), except for EXTEND HAND, they are labelled differently because details based on personal observations have been added.

ACCEPTED MANUSCRIPT

Table 2. Characteristics of each gesture for both chimpanzees and gorillas

| Gesture | Sensory modality | Object manipulation | Duration | Sharing degree |
|-------------------------|------------------|---------------------|----------|-----------------------|
| BEAT BODY (g) | Auditory | No | Short | Common |
| BEAT CHEST (g) | Auditory | No | Short | Rare |
| CLAP HAND | Auditory | No | Short | Rare |
| SLAP FOOT (c) | Auditory | No | Short | Common |
| SLAP HAND | Auditory | No | Short | Common |
| EMBRACE | Tactile | No | Long | Common (c) / Rare (g) |
| EMBRACE HALF | Tactile | No | Long | Rare |
| EMBRACE LATERAL | Tactile | No | Long | Common |
| EMBRACE VENTRAL/DORSAL | Tactile | No | Long | Rare |
| HAND ON (c) | Tactile | No | Long | Common |
| HIT WITH OBJECT (c) | Tactile | Yes | Short | Rare |
| KICK (c) | Tactile | No | Short | Rare |
| PUNCH | Tactile | No | Short | Common |
| PUSH (c) | Tactile | No | Short | Common |
| TOUCH BODY | Tactile | No | Long | Common |
| TOUCH GENITAL (c) | Tactile | No | Long | Common |
| ATTEMPT TO REACH | Visual | No | Short | Common |
| DRAG OBJECT | Visual | Yes | Long | Rare |
| EXTEND HAND (c) | Visual | No | Long | Common |
| PUT OBJECT ON HEAD/BACK | Visual | Yes | Short | Rare |
| RAISE ARM | Visual | No | Short | Common |
| SHAKE OBJECT | Visual | Yes | Short | Common |
| THROW OBJECT | Visual | Yes | Short | Rare |

Gestures are regrouped by sensory modality. (c) refers to chimpanzees only; (g) refers to gorillas only. Object manipulation refers to gestures involving the use of an object (“Yes”) or not (“No”). Duration refers to gestures lasting less than 2 seconds (“Short”) or more than 2 seconds (“Long”). Sharing degree refers to rare gestures performed by only a few subjects in the population (“Rare”) or to common gestures performed by most of the subjects in the population (“Common”).

Table 3. Generalized linear mixed model with dependent, fixed and random variables, their type and associated levels

| Name | Type |
|--|---|
| Dependent variable | |
| Hand use | Dichotomous (L/R) |
| Fixed variables | |
| Individual characteristics | |
| Position of recipient in signaller's visual field during interaction (SVF) | Dichotomous (L/R) |
| Position of signaller in recipient's visual field during interaction (RVF) | Dichotomous (L/R) |
| Emotional context of interaction | Dichotomous (Negative/Positive) |
| Signaller's sex | Dichotomous (F/M) |
| Signaller's age class | Ordinal (Immature/Adolescent/Young adult/Mature adult) |
| Recipient's sex | Dichotomous (F/M) |
| Recipient's age class | Ordinal (Immature /Adolescent/Young adult/Mature adult) |
| Zoo | Nominal (Beauval/Leipzig/Palmyre) |
| Species | Nominal (Chimpanzee/Gorilla) |
| Signaller's hierarchical rank | Ordinal (Dominant/Intermediate/Subordinate) |
| Recipient's hierarchical rank | Ordinal (Dominant/Intermediate/Subordinate) |
| Kinship | Nominal (Parent-infant/Siblings/Unrelated) |
| Affiliation | Ordinal (Low/Medium/Strong) |
| Gesture characteristics | |
| Sensory modality | Nominal (Auditory/Tactile/Visual) |
| Communication tool | Dichotomous (Yes/No) |
| Duration | Dichotomous (Short/Long) |
| Sharing degree | Dichotomous (Rare/Common) |
| Random variables | |
| Signaller's identity | Nominal |
| Recipient's identity | Nominal |

L: Left; R: Right; F: Female; M: Male.

Table 4. Comparisons between Mean Absolute values of Handedness Index score (Mean ABSHIs +/- S.E.) of stable and non-stable subjects for chimpanzees and gorillas

| | Chimpanzees | | | | Gorillas | | | |
|-------------------------|---------------|---------------|-------------------|-----------|----------------------|----------------------|-------------------|------------------|
| | Stable | Unstable | Mann-Whitney test | | Stable | Unstable | Mann-Whitney test | |
| CLAP HAND | 0.85. | 0.74+/- 0.11 | | | 0.64 +/- 0.12 | 0.81+/- 0.11 | U = 4 | P = 0.393 |
| SLAP FOOT | 0.55 +/-0.10 | 0.40 +/- 0.10 | U = 0.923 | P = 0.337 | | | | |
| SLAP HAND | 0.53 +/- 0.05 | 0.30 +/- 0.09 | U = 2.077 | P = 0.150 | 0.70 +/- 0.09 | 0.34 +/- 0.21 | U = 15 | P = 0.167 |
| EMBRACE | 0.27 +/- 0.10 | 0.27 +/- 0.06 | U = 0.410 | P = 0.522 | 0.13 +/- 0.07 | 0.34 +/- 0.17 | U = 3 | P = 0.25 |
| EMBRACE HALF | 0.17 +/- 0.03 | 0.17 +/- 0.05 | U = 0.176 | P = 0.675 | 0.38 +/- 0.29 | 0.30 +/- 0.21 | | |
| EMBRACE LATERAL | 0.24 +/- 0.06 | 0.21 +/- 0.11 | U = 1.256 | P = 0.262 | 0.19 +/- 0.07 | 0.12 +/- 0.07 | U = 11 | P = 0.714 |
| EMBRACE VENTRAL/DORSAL | 0.16 +/- 0.08 | 0.21 +/- 0.04 | U = 1.143 | P = 0.285 | 0.51 +/- 0.05 | 0.31 +/- 0.11 | | |
| HAND ON | 0.16 +/- 0.05 | 0.36 +/- 0.11 | U = 1.641 | P = 0.200 | | | | |
| HIT WITH OBJECT | 0.41 +/- 0.05 | 0.53 +/- 0.18 | U = 0.021 | P = 0.885 | | | | |
| KICK | 0.37 +/- 0.09 | 0.03 +/- 0.03 | U = 3.75 | P = 0.053 | | | | |
| PUNCH | 0.37 +/- 0.05 | 0.33 +/- 0.04 | U = 0.103 | P = 0.749 | 0.34 +/- 0.04 | 0.28 +/- 0.07 | U = 12 | P = 0.548 |
| PUSH | 0.31 +/- 0.12 | 0.20 +/- 0.10 | U = 0.54 | P = 0.462 | | | | |
| TOUCH BODY | 0.07 +/- 0.04 | 0.08 +/- 0.03 | U = 0 | P = 1 | 0.19 +/- 0.05 | 0.02 +/- 0.01 | U = 18 | P = 0.024 |
| TOUCH GENITAL | 0.16 +/- 0.06 | 0.34 +/- 0.15 | U = 0.923 | P = 0.337 | | | | |
| ATTEMPT TO REACH | 0.36 +/- 0.08 | 0.24 +/- 0.09 | U = 0.923 | P = 0.337 | 0.38 +/- 0.05 | 0.17 +/- 0.06 | U = 16 | P = 0.095 |
| DRAG OBJECT | 0.33 +/- 0.10 | 0.22 +/- 0.05 | U = 0.176 | P = 0.675 | 0.30 +/- 0.10 | 0.55 +/- 0.18 | U = 3 | P = 0.4 |
| EXTEND HAND | 0.43 +/- 0.15 | 0.26 +/- 0.07 | U = 1.013 | P = 0.314 | | | | |
| PUT OBJECT ON HEAD/BACK | 0.39 +/- 0.13 | 0.32 +/- 0.09 | U = 0.06 | P = 0.807 | 0.39 +/- 0.06 | 0.08 +/- 0.03 | U = 18 | P = 0.024 |
| RAISE ARM | 0.48 +/- 0.08 | 0.47 +/- 0.10 | U = 0.006 | P = 0.936 | 0.46 +/- 0.10 | 0.35 +/- 0.03 | U = 14 | P = 0.262 |
| SHAKE OBJECT | 0.29 +/- 0.02 | 0.30 +/- 0.04 | U = 0.103 | P = 0.749 | 0.45 +/- 0.08 | 0.14 +/- 0.05 | U = 18 | P = 0.024 |
| THROW OBJECT | 0.52 +/- 0.15 | 0.58 +/- 0.10 | U = 0.011 | P = 0.917 | 0.28 +/- 0.04 | 0.08 +/- 0.04 | U = 10 | P = 0.286 |
| BEAT BODY | | | | | 0.46 +/- 0.17 | 0.27 +/- 0.15 | U = 8 | P = 0.629 |
| BEAT CHEST | | | | | 0.53 +/- 0.10 | 0.47 +/- 0.06 | U = 11 | P = 0.714 |

Gestures are regrouped by sensory modality (for chimpanzees: 3 auditory, 11 tactile and 7 visual gestures; for gorillas: 4 auditory, 6 tactile and 6 visual gestures) and presented by alphabetic order. Gestures are regrouped by sensory modality (3 auditory, 11 tactile and 7 visual gestures). -: insufficient number of subjects who performed at least 6 times each the given gesture for testing; Mann-Whitney test: U-value and p-value of the Mann-Whitney test performed on the ABSHI values of stable versus non-stable subjects. Significant results are in bold.

Table 5. Comparisons of Handedness Index score (HI) and Absolute of Handedness Index score (ABSHI) values between chimpanzee and gorilla subjects

| Gesture | Mann-Whitney test | | Mann-Whitney test | |
|-------------------------|-------------------|-------------------------|-------------------|--------------------------|
| | HI values | | ABSHI values | |
| CLAP HAND | U = 0.018 | <i>P</i> = 0.894 | U = 2.137 | <i>P</i> = 0.144 |
| SLAP HAND | U = 4.92 | <i>P</i> = 0.027 | U = 3.539 | <i>P</i> = 0.060 |
| EMBRACE | U = 0.774 | <i>P</i> = 0.379 | U = 1.758 | <i>P</i> = 0.185 |
| EMBRACE HALF | U = 0.073 | <i>P</i> = 0.787 | U = 0.336 | <i>P</i> = 0.562 |
| EMBRACE LATERAL | U = 0.065 | <i>P</i> = 0.798 | U = 0.873 | <i>P</i> = 0.350 |
| EMBRACE VENTRAL/DORSAL | U = 2.103 | <i>P</i> = 0.147 | U = 1.264 | <i>P</i> = 0.261 |
| PUNCH | U = 0.186 | <i>P</i> = 0.666 | U = 0.312 | <i>P</i> = 0.576 |
| TOUCH BODY | U = 0.488 | <i>P</i> = 0.485 | U = 1.702 | <i>P</i> = 0.192 |
| ATTEMPT TO REACH | U = 0.256 | <i>P</i> = 0.613 | U = 0.027 | <i>P</i> = 0.871 |
| DRAG OBJECT | U = 0.851 | <i>P</i> = 0.356 | U = 1.090 | <i>P</i> = 0.297 |
| PUT OBJECT ON HEAD/BACK | U = 0.585 | <i>P</i> = 0.444 | U = 1.776 | <i>P</i> = 0.183 |
| RAISE ARM | U = 1.889 | <i>P</i> = 0.169 | U = 2.752 | <i>P</i> = 0.097 |
| SHAKE OBJECT | U = 0.015 | <i>P</i> = 0.902 | U = 0.142 | <i>P</i> = 0.707 |
| THROW OBJECT | U = 7.610 | <i>P</i> = 0.006 | U = 13.231 | <i>P</i> = 0.0003 |

Gestures shared by both species are regrouped by sensory modality (2 auditory, 6 tactile and 6 visual gestures) and presented by alphabetic order. Mann-Whitney test: U-value and p-value of the Mann-Whitney test performed on the HI and ABSHI values of chimpanzee versus gorilla subjects. Significant results are in bold.

Table 6. Analysis of deviance table (Type II Wald chi-square tests)

| <i>Fixed terms and associated interactions</i> | χ^2 | <i>Df</i> | <i>P</i> |
|--|----------|-----------|--------------------|
| Species | 0.933 | 1 | 0.334 |
| Gesture sensory modality | 352.325 | 2 | <2.2e-16 |
| Signaller's age class | 1.510 | 3 | 0.680 |
| Signaller Visual Field during interaction (SVF) | 3437.558 | 1 | <2.2e-16 |
| Recipient Visual Field during interaction (RVF) | 113.069 | 1 | <2.2e-16 |
| Signaller's hierarchical rank | 0.877 | 2 | 0.645 |
| Emotional context | 29.778 | 1 | 4.844e-08 |
| Object manipulation gesture | 2.137 | 1 | 0.144 |
| Signaller's sex | 2.566 | 1 | 0.109 |
| Species × Gesture sensory modality | 35.441 | 2 | 2.014e-08 |
| Species × Signaller's age class | 6.257 | 3 | 0.100 |
| Species × SVF | 38.512 | 1 | 5.442e-10 |
| Species × RVF | 3.083 | 1 | 0.079 |
| Gesture sensory modality × Signaller's age class | 36.335 | 6 | 2.373e-06 |
| Gesture sensory modality × Signaller's hierarchical rank | 14.509 | 4 | 0.006 |
| Gesture sensory modality × SVF | 1714.496 | 2 | <2.2e-16 |
| Gesture sensory modality × RVF | 92.142 | 2 | <2.2e-16 |
| Gesture sensory modality × Emotion context | 42.005 | 2 | 7.564e-10 |
| Object manipulation gesture × Signaller's sex | 24.064 | 1 | 9.318e-07 |
| SVF × Object manipulation gesture | 478.309 | 1 | <2.2e-16 |
| RVF × Object manipulation gesture | 4.002 | 1 | 0.045 |
| Emotion context × Object manipulation gesture | 8.971 | 1 | 0.003 |
| SVF × Signaller's sex | 14.681 | 1 | 0.0001 |
| SVF × Signaller's hierarchical rank | 7.454 | 2 | 0.024 |
| RVF × Emotion context | 8.932 | 1 | 0.003 |

χ^2 : value of the type II Wald chisquare; Df: Degree of freedom; *P*: p-value of the type II Wald chisquare. Significant results are in bold.

Table A1. Descriptive statistics and analyses for each stable chimpanzee subject

| Stable subject | Lukombe | | | Cheetah | | | Tumba | | | Wamba | | | Kofi | | | Benji | | | |
|-------------------------|---------|--------------|--------------|---------|--------------|--------------|--------|---------------|--------------|--------|---------------|--------------|--------|---------------|--------------|--------------|---------------|--------------|--|
| | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | |
| Gesture | | | | | | | | | | | | | | | | | | | |
| CLAP HAND | | - | | | - | | | - | | | - | | -0.851 | 0 | LH | | - | | |
| SLAP FOOT | 0.759 | 0 | RH | 0.568 | 0 | RH | 0.064 | 0.471 | n.l. | 0.546 | 0.0004 | RH | 0.700 | 0 | RH | 0.667 | 0.0003 | RH | |
| SLAP HAND | 0.484 | 0 | RH | 0.444 | 0 | RH | 0.538 | 0 | RH | 0.494 | 0 | RH | 0.432 | 0 | RH | 0.765 | 0 | RH | |
| EMBRACE | 0.152 | 0.487 | n.l. | 0.045 | 0.807 | n.l. | 0.704 | 0.0003 | RH | 0.429 | 0.180 | n.l. | 0.130 | 0.461 | n.l. | 0.143 | 0.572 | n.l. | |
| EMBRACE HALF | 0.261 | 0.104 | n.l. | 0.137 | 0.029 | RH | -0.077 | 1 | n.l. | 0.167 | 0.774 | n.l. | 0.188 | 0.377 | n.l. | | - | | |
| EMBRACE LATERAL | 0.358 | 0.002 | RH | -0.200 | 0.064 | n.l. | 0.103 | 0.711 | n.l. | 0.111 | 0.618 | n.l. | 0.231 | 0.016 | RH | 0.455 | 0.0525 | RH | |
| EMBRACE VENTRAL/DORSAL | 0 | 1 | n.l. | 0.095 | 0.644 | n.l. | 0.077 | 0.749 | n.l. | 0.000 | 1 | n.l. | 0.529 | 0.049 | RH | -0.250 | 0.727 | n.l. | |
| HAND ON | -0.263 | 0.359 | n.l. | -0.045 | 0.807 | n.l. | -0.115 | 0.489 | n.l. | 0.048 | 1 | n.l. | -0.177 | 0.392 | n.l. | 0.333 | 0.508 | n.l. | |
| HIT WITH OBJECT | 0.400 | 0.344 | n.l. | | - | | 0.539 | 0.092 | n.l. | 0.286 | 0.424 | n.l. | 0.419 | 0.029 | RH | | - | | |
| KICK | 0.600 | 0.109 | n.l. | 0.250 | 0.727 | n.l. | 0.100 | 0.824 | n.l. | 0.556 | 0.180 | n.l. | 0.333 | 0.388 | n.l. | | - | | |
| PUNCH | 0.271 | 0.003 | RH | 0.228 | 0.019 | RH | 0.365 | 0 | RH | 0.360 | 0.108 | n.l. | 0.445 | 0 | RH | 0.543 | 0.002 | RH | |
| PUSH | | - | | 0.429 | 0.453 | n.l. | 0.177 | 0.629 | n.l. | | - | | -0.048 | 1 | n.l. | 0.571 | 0.004 | RH | |
| TOUCH BODY | -0.039 | 0.654 | n.l. | -0.026 | 0.594 | n.l. | 0.007 | 1 | n.l. | 0.053 | 0.731 | n.l. | 0.031 | 0.721 | n.l. | 0.275 | 0.030 | RH | |
| TOUCH GENITAL | 0.442 | 0.005 | RH | 0.177 | 0.629 | n.l. | -0.022 | 0.917 | n.l. | -0.103 | 0.711 | n.l. | -0.073 | 0.631 | n.l. | -0.120 | 0.690 | n.l. | |
| ATTEMPT TO REACH | 0.297 | 0.099 | n.l. | 0.306 | 0.044 | RH | 0.313 | 0.017 | RH | 0.289 | 0.073 | n.l. | 0.170 | 0.272 | n.l. | 0.762 | 0 | RH | |
| DRAG OBJECT | 0.167 | 0.245 | n.l. | -0.200 | 0.424 | n.l. | 0.155 | 0.235 | n.l. | 0.608 | 0 | RH | 0.520 | 0.0003 | RH | | - | | |
| EXTEND HAND | 0.143 | 1 | n.l. | 0.299 | 0.001 | RH | 0.286 | 0.023 | RH | | - | | 0.426 | 0 | RH | 1 | 0 | RH | |
| PUT OBJECT ON HEAD/BACK | -0.029 | 1 | n.l. | 0.349 | 0.002 | RH | 0.200 | 0.424 | n.l. | 0.769 | 0.0001 | RH | 0.594 | 0 | RH | | - | | |
| RAISE ARM | 0.217 | 0.184 | n.l. | 0.313 | 0.017 | RH | 0.546 | 0 | RH | 0.714 | 0.125 | n.l. | 0.519 | 0 | RH | 0.600 | 0.0001 | RH | |
| SHAKE OBJECT | 0.238 | 0 | RH | 0.354 | 0 | RH | 0.252 | 0 | RH | 0.221 | 0.0004 | RH | 0.351 | 0 | RH | 0.333 | 0.302 | n.l. | |
| THROW OBJECT | 0.300 | 0.263 | n.l. | 0.875 | 0.001 | RH | -0.136 | 0.266 | n.l. | 0.875 | 0.001 | RH | 0.429 | 0.004 | RH | | - | | |
| Nb n.l. | | | 13 | | | 9 | | | 13 | | | 12 | | | 8 | | | 5 | |
| Nb RH | | | 6 | | | 10 | | | 7 | | | 6 | | | 12 | | | 9 | |
| Nb LH | | | 0 | | | 0 | | | 0 | | | 0 | | | 1 | | | 0 | |
| B test Nb LH vs. Nb RH | | | 0.031 | | | 0.002 | | | 0.016 | | | 0.031 | | | 0.003 | | | 0.004 | |

Gestures are regrouped by sensory modality (3 auditory, 11 tactile and 7 visual gestures) and presented by alphabetic order. HI: Handedness Index score of the subject, the sign indicates the direction of the gestural bias (negative value: left-hand bias, positive value: right-hand bias). B test: p-value of the binomial test on the numbers of left-hand versus right-hand responses; -: insufficient number of hand responses for testing; Lat: direction of lateral hand bias; RH: right-hand bias; LH: Left-hand bias; n.l.: non-lateralized; Nb n.l.: number of gestures for which the subject is non-lateralized; Nb RH: number of gestures for which the subject is right-handed; Nb LH: number of gestures for which the subject is left-handed; B test Nb LH vs. Nb RH: p-value of the binomial test on the numbers of left-lateralized versus right-lateralized gestures. Significant results are in bold.

Table A2. Descriptive statistics and analyses for each non-stable chimpanzee subject

| Non-stable subject | Bangolo | | | Kelle | | | Lobo | | | Lulu | | | Frodo | | | Joseph | | | |
|-------------------------|---------|--------------|-------|--------------|---------------|-----------|--------|--------------|-------|--------|--------------|-------|--------|---------------|-------|---------------|---------------|-----------|--|
| | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | |
| Gesture | | | | | | | | | | | | | | | | | | | |
| CLAP HAND | -0.808 | 0 | LH | | - | | -0.529 | 0.049 | LH | | - | | -0.873 | 0 | LH | | - | | |
| SLAP FOOT | 0.128 | 0.308 | n.l. | 0.540 | 0 | RH | -0.273 | 0.549 | n.l. | 0.588 | 0 | RH | 0.714 | 0.002 | RH | 0.152 | 0.175 | n.l. | |
| SLAP HAND | 0.254 | 0 | RH | 0.623 | 0 | RH | 0.143 | 0.230 | n.l. | 0.504 | 0 | RH | 0.075 | 0.625 | n.l. | 0.191 | 0.101 | n.l. | |
| EMBRACE | 0.071 | 0.547 | n.l. | -0.178 | 0.160 | n.l. | 0.267 | 0.201 | n.l. | -0.395 | 0.014 | LH | 0.234 | 0.144 | n.l. | -0.455 | 0.0525 | LH | |
| EMBRACE HALF | 0.086 | 0.505 | n.l. | -0.167 | 0.541 | n.l. | -0.091 | 0.728 | n.l. | -0.120 | 0.480 | n.l. | 0.375 | 0.210 | n.l. | | - | | |
| EMBRACE LATERAL | 0.106 | 0.166 | n.l. | -0.044 | 0.707 | n.l. | -0.158 | 0.207 | n.l. | -0.130 | 0.336 | n.l. | 0.059 | 0.665 | n.l. | -0.750 | 0.070 | n.l. | |
| EMBRACE VENTRAL/DORSAL | 0.304 | 0 | RH | -0.170 | 0.019 | LH | 0.111 | 1 | n.l. | -0.240 | 0.119 | n.l. | | - | | | - | | |
| HAND ON | -0.091 | 0.652 | n.l. | -0.097 | 0.720 | n.l. | -0.733 | 0.007 | LH | -0.400 | 0.043 | LH | 0.222 | 0.243 | n.l. | -0.600 | 0.035 | LH | |
| HIT WITH OBJECT | 0.765 | 0.002 | RH | -0.150 | 0.219 | n.l. | 0.286 | 0.424 | n.l. | | - | | 0.909 | 0 | RH | | - | | |
| KICK | 0.059 | 1 | n.l. | | - | | | - | | 0 | 1 | n.l. | | - | | | - | | |
| PUNCH | 0.320 | 0 | RH | 0.385 | 0.001 | RH | -0.171 | 0.349 | n.l. | 0.414 | 0 | RH | 0.411 | 0 | RH | -0.304 | 0.210 | n.l. | |
| PUSH | 0 | 1 | n.l. | 0.455 | 0.0525 | RH | -0.077 | 1 | n.l. | -0.053 | 1 | n.l. | | - | | -0.400 | 0.115 | n.l. | |
| TOUCH BODY | -0.002 | 1 | n.l. | 0.006 | 0.955 | n.l. | -0.226 | 0.038 | LH | -0.034 | 0.601 | n.l. | -0.109 | 0.250 | n.l. | -0.111 | 0.618 | n.l. | |
| TOUCH GENITAL | -0.039 | 0.820 | n.l. | -0.250 | 0.455 | n.l. | -0.478 | 0.002 | LH | -0.238 | 0.164 | n.l. | -0.056 | 0.868 | n.l. | -1 | 0.0001 | LH | |
| ATTEMPT TO REACH | 0.048 | 0.878 | n.l. | 0.174 | 0.302 | n.l. | 0.026 | 1 | n.l. | 0.326 | 0.003 | RH | 0.241 | 0.265 | n.l. | -0.615 | 0.003 | LH | |
| DRAG OBJECT | 0.231 | 0.082 | n.l. | 0.167 | 0.312 | n.l. | 0.310 | 0.136 | n.l. | 0.056 | 0.868 | n.l. | 0.333 | 0.688 | n.l. | | - | | |
| EXTEND HAND | 0.286 | 0.424 | n.l. | 0.515 | 0.005 | RH | 0.273 | 0.096 | n.l. | 0.037 | 0.892 | n.l. | 0.344 | 0.0001 | RH | -0.077 | 0.845 | n.l. | |
| PUT OBJECT ON HEAD/BACK | 0.391 | 0.002 | RH | 0.064 | 0.771 | n.l. | 0.333 | 0.508 | n.l. | -0.500 | 0.289 | n.l. | | - | | | - | | |
| RAISE ARM | 0.540 | 0 | RH | 0.313 | 0.110 | n.l. | 0.368 | 0.034 | RH | -0.103 | 0.711 | n.l. | 0.698 | 0 | RH | 0.778 | 0 | RH | |
| SHAKE OBJECT | 0.302 | 0 | RH | 0.240 | 0 | RH | 0.260 | 0 | RH | 0.182 | 0.001 | RH | 0.389 | 0 | RH | -0.421 | 0 | LH | |
| THROW OBJECT | 0.280 | 0.230 | n.l. | 0.556 | 0.180 | n.l. | | - | | 0.500 | 0.289 | n.l. | 0.690 | 0 | RH | -0.871 | 0 | LH | |
| Nb n.l. | | | 13 | | | 12 | | | 13 | | | 12 | | | 9 | | | 7 | |
| Nb RH | | | 7 | | | 6 | | | 2 | | | 5 | | | 7 | | | 1 | |
| Nb LH | | | 1 | | | 1 | | | 4 | | | 2 | | | 1 | | | 6 | |
| B test Nb LH vs. Nb RH | | | 0.070 | | | 0.125 | | | 0.688 | | | 0.453 | | | 0.070 | | | 0.125 | |

Gestures are regrouped by sensory modality (3 auditory, 11 tactile and 7 visual gestures) and presented by alphabetic order. HI: Handedness Index score of the subject, the sign indicates the direction of the gestural bias (negative value: left-hand bias, positive value: right-hand bias); B test: p-value of the binomial test on the numbers of left-hand versus right-hand responses; -: insufficient number of hand responses for testing; Lat: direction of lateral hand bias; RH: right-hand bias; LH: Left-hand bias; n.l.: non-lateralized; Nb n.l.: number of gestures for which the subject is non-lateralized; Nb RH: number of gestures for which the subject is right-handed; Nb LH: number of gestures for which the subject is left-handed; B test Nb LH vs. Nb RH: p-value of the binomial test on the numbers of left-lateralized versus right-lateralized gestures. Significant results are in bold.

Table A3. Descriptive statistics and analyses for each stable gorilla subject

| Stable gorilla subject | Tayari | | | Chama | | | Touni | | | Miliki | | | Lomako | | | Shailâ | | |
|-------------------------|--------|--------------|--------------|--------|--------------|--------------|-------|---------------|--------------|--------------|---------------|--------------|--------|--------------|--------------|--------|---------------|--------------|
| | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat | HI | B | Lat | HI | B test | Lat |
| BEAT BODY | 0.44 | 0.003 | RH | -0.081 | 0.743 | n.l. | - | | | - | | | 0.9 | 0 | RH | 0.429 | 0.180 | n.l. |
| BEAT CHEST | 0.532 | 0 | RH | -0.130 | 0.251 | n.l. | 0.316 | 0.008 | RH | 0.724 | 0.0001 | RH | 0.776 | 0 | RH | 0.68 | 0 | RH |
| CLAP HAND | 0.571 | 0 | RH | 0.829 | 0 | RH | 0.535 | 0.001 | RH | -0.286 | 0.424 | n.l. | 1 | 0.004 | RH | | - | |
| SLAP HAND | 0.481 | 0 | RH | 0.430 | 0 | RH | 0.655 | 0 | RH | 1 | 0.001 | RH | 0.811 | 0 | RH | 0.824 | 0 | RH |
| EMBRACE | -0.143 | 1 | n.l. | 0 | 1 | n.l. | 0.4 | 0.115 | n.l. | | - | | 0.035 | 1 | n.l. | -0.05 | 0.875 | n.l. |
| EMBRACE HALF | -0.091 | 1 | n.l. | | - | | | - | | 0.667 | 0.219 | n.l. | | | | | - | |
| EMBRACE LATERAL | 0.05 | 0.875 | n.l. | 0.25 | 0.154 | n.l. | 0.167 | 0.541 | n.l. | 0.455 | 0.0525 | RH | 0 | 1 | n.l. | 0.213 | 0.124 | n.l. |
| EMBRACE VENTRAL/DORSAL | | - | | | - | | 0.455 | 0.227 | n.l. | | - | | 0.556 | 0.180 | n.l. | | - | |
| PUNCH | 0.340 | 0.001 | RH | 0.349 | 0.002 | RH | 0.222 | 0.016 | RH | 0.429 | 0.002 | RH | 0.487 | 0 | RH | 0.233 | 0.009 | RH |
| TOUCH BODY | 0.241 | 0.012 | RH | 0.054 | 0.679 | n.l. | 0.169 | 0.137 | n.l. | 0.333 | 0.0533 | RH | 0.294 | 0.009 | RH | -0.073 | 0.331 | n.l. |
| ATTEMPT TO REACH | 0.5 | 0.004 | RH | 0.259 | 0.248 | n.l. | 0.5 | 0.023 | RH | 0.429 | 0.453 | n.l. | -0.280 | 0.230 | n.l. | 0.302 | 0.066 | n.l. |
| DRAG OBJECT | 0.365 | 0 | RH | 0.462 | 0.029 | RH | | - | | | - | | 0 | 1 | n.l. | 0.371 | 0.003 | RH |
| PUT OBJECT ON HEAD/BACK | 0.415 | 0 | RH | 0.214 | 0.345 | n.l. | 0.395 | 0.001 | RH | 0.6 | 0.109 | n.l. | 0.240 | 0.119 | n.l. | 0.5 | 0.0001 | RH |
| RAISE ARM | 0.403 | 0.001 | RH | 0.623 | 0 | RH | 0.477 | 0.0002 | RH | 0.7 | 0.003 | RH | 0.543 | 0 | RH | 0 | 1 | n.l. |
| SHAKE OBJECT | 0.317 | 0 | RH | 0.402 | 0 | RH | 0.467 | 0.016 | RH | 0.846 | 0.003 | RH | 0.321 | 0.027 | RH | 0.348 | 0 | RH |
| THROW OBJECT | 0.2 | 0.362 | n.l. | 0.429 | 0.036 | RH | 0.25 | 0.455 | n.l. | | - | | 0.290 | 0.015 | RH | 0.217 | 0.047 | RH |
| Nb n.l. | | | 4 | | | 7 | | | 5 | | | 4 | | | 6 | | | 6 |
| Nb RH | | | 11 | | | 7 | | | 8 | | | 7 | | | 9 | | | 7 |
| Nb LH | | | 0 | | | 0 | | | 0 | | | 0 | | | 0 | | | 0 |
| B test Nb LH vs. Nb RH | | | 0.001 | | | 0.016 | | | 0.008 | | | 0.016 | | | 0.004 | | | 0.016 |

Gestures are regrouped by sensory modality (4 auditory, 6 tactile and 6 visual gestures) and presented by alphabetic order. HI: Handedness Index score of the subject, the sign indicates the direction of the gestural bias (negative value: left-hand bias, positive value: right-hand bias); B test: p-value of the binomial test on the numbers of left-hand versus right-hand responses; -: insufficient number of hand responses for testing; Lat: direction of lateral hand bias; RH: right-hand bias; LH: Left-hand bias; n.l.: non-lateralized; Nb n.l.: number of gestures for which the subject is non-lateralized; Nb RH: number of gestures for which the subject is right-handed; Nb LH: number of gestures for which the subject is left-handed; B test Nb LH vs. Nb RH: p-value of the binomial test on the numbers of left-lateralized versus right-lateralized gestures. Significant results are in bold.

Table A4. Descriptive statistics and analyses for each non-stable gorilla subject

| Non-stable gorilla subject | Mzungu | | | N'Washi | | | N'Akouh | | |
|----------------------------|--------|---------------|------|---------|---------------|-------|--------------|---------------|-----------|
| | HI | B test | Lat | HI | B test | Lat | HI | B test | Lat |
| BEAT BODY | -0.030 | 1 | n.l. | -0.238 | 0.383 | n.l. | -0.539 | 0.092 | n.l. |
| BEAT CHEST | 0.348 | 0 | RH | -0.539 | 0 | LH | -0.510 | 0 | LH |
| CLAP HAND | 0.951 | 0 | RH | 0.895 | 0.0001 | RH | 0.586 | 0.002 | RH |
| SLAP HAND | 0.763 | 0 | RH | 0.133 | 0.132 | n.l. | 0.132 | 0.207 | n.l. |
| EMBRACE | 0.647 | 0.013 | RH | 0.067 | 0.856 | n.l. | 0.292 | 0.025 | RH |
| EMBRACE HALF | -0.714 | 0.002 | LH | -0.177 | 0.629 | n.l. | 0 | 1 | n.l. |
| EMBRACE LATERAL | -0.243 | 0.018 | LH | -0.013 | 0.937 | n.l. | 0.103 | 0.133 | n.l. |
| EMBRACE VENTRAL/DORSAL | 0.429 | 0.453 | n.l. | - | - | - | 0.2 | 0.607 | n.l. |
| PUNCH | -0.306 | 0.013 | LH | 0.386 | 0.0004 | RH | 0.161 | 0.0535 | RH |
| TOUCH BODY | -0.032 | 0.685 | n.l. | 0.008 | 0.918 | n.l. | -0.018 | 0.785 | n.l. |
| ATTEMPT TO REACH | -0.289 | 0.073 | n.l. | 0.103 | 0.711 | n.l. | -0.130 | 0.461 | n.l. |
| DRAG OBJECT | -0.647 | 0.0002 | LH | 0.8 | 0.022 | RH | 0.214 | 0.141 | n.l. |
| PUT OBJECT ON HEAD/BACK | -0.067 | 1 | n.l. | 0.048 | 0.801 | n.l. | 0.135 | 0.511 | n.l. |
| RAISE ARM | -0.288 | 0.019 | LH | 0.407 | 0.004 | RH | 0.352 | 0.004 | RH |
| SHAKE OBJECT | 0.042 | 0.813 | n.l. | 0.182 | 0.045 | RH | 0.202 | 0.001 | RH |
| THROW OBJECT | 0 | 1 | n.l. | -0.118 | 0.608 | n.l. | 0.129 | 0.232 | n.l. |
| Nb n.l. | | | 7 | | | | | | 10 |
| Nb RH | | | 4 | | | 5 | | | 5 |
| Nb LH | | | 5 | | | 1 | | | 1 |
| B test Nb LH vs. Nb RH | | | 1 | | | 0.219 | | | 0.219 |

Gestures are regrouped by sensory modality (4 auditory, 6 tactile and 6 visual gestures) and presented by alphabetic order. HI: Handedness Index score of the subject, the sign indicates the direction of the gestural bias (negative value: left-hand bias, positive value: right-hand bias); B test: p-value of the binomial test on the numbers of left-hand versus right-hand responses; -: insufficient number of hand responses for testing; Lat: direction of lateral hand bias; RH: right-hand bias; LH: Left-hand bias; n.l.: non-lateralized; Nb n.l.: number of gestures for which the subject is non-lateralized; Nb RH: number of gestures for which the subject is right-handed; Nb LH: number of gestures for which the subject is left-handed; B test Nb LH vs. Nb RH: p-value of the binomial test on the numbers of left-lateralized versus right-lateralized gestures. Significant results are in bold.

Table A5. Results of post-hoc multiple comparisons tests

| Species × Sensory modality | | | | | |
|---|----------------------|----------|-------|---------|------------------|
| contrast | | estimate | SE | z,ratio | <i>P</i> |
| Chimpanzee,Auditory | - Gorilla,Auditory | -0.411 | 0.108 | -3.802 | 0.002 |
| Chimpanzee,Tactile | - Gorilla,Tactile | -0.056 | 0.095 | -0.586 | 0.992 |
| Chimpanzee,Visual | - Gorilla,Visual | 0.057 | 0.096 | 0.594 | 0.992 |
| Chimpanzee,Auditory | - Chimpanzee,Tactile | -0.043 | 0.091 | -0.476 | 0.997 |
| Chimpanzee,Auditory | - Chimpanzee,Visual | -0.383 | 0.090 | -4.247 | 0.0003 |
| Chimpanzee,Tactile | - Chimpanzee,Visual | -0.339 | 0.094 | -3.594 | 0.004 |
| Gorilla,Auditory | - Gorilla,Tactile | 0.311 | 0.105 | 2.975 | 0.035 |
| Gorilla,Auditory | - Gorilla,Visual | 0.085 | 0.102 | 0.833 | 0.961 |
| Gorilla,Tactile | - Gorilla,Visual | -0.227 | 0.100 | -2.277 | 0.204 |
| Species × Signaller Visual Field during interaction | | | | | |
| contrast | | estimate | SE | z,ratio | <i>P</i> |
| Chimpanzee,R | - Gorilla,R | 0.041 | 0.095 | 0.434 | 0.973 |
| Chimpanzee,L | - Gorilla,L | -0.314 | 0.093 | -3.378 | 0.004 |
| Chimpanzee,R | - Chimpanzee,L | 1.173 | 0.046 | 25.574 | <.0001 |
| Gorilla,R | - Gorilla,L | 0.818 | 0.056 | 14.725 | <.0001 |

L: Left; R: Right; estimate: difference between LSmeans SE: Standard Error of the difference; z.ratio: ratio of the estimate to its standard error; *P*: Tukey's p-value. Significant results are in bold.

- Both species show either stability or flexibility in their gestural laterality
- Link between stability of the direction and strength of gestural laterality
- The position of interactants and sensory modality influence gestural laterality
- The species social structure and dynamics may have impacted gestural laterality
- Social pressures may have shaped laterality through natural selection

ACCEPTED MANUSCRIPT