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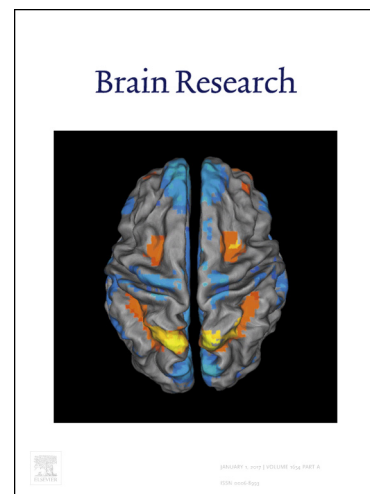
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Intraspecific gestural laterality in chimpanzees and gorillas and the impact of social propensities

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).

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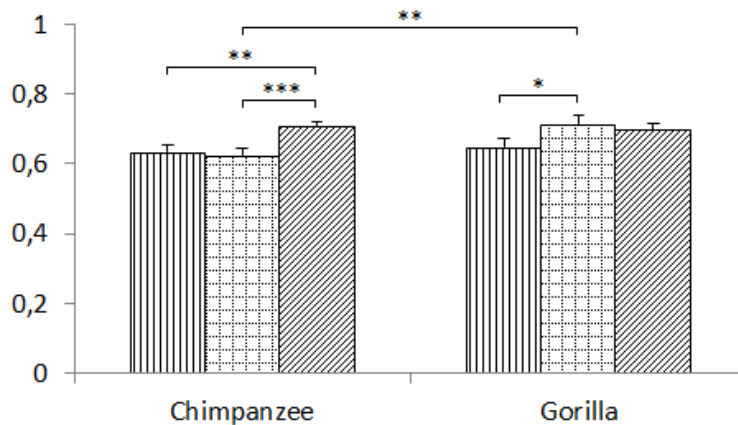
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Figure 1

a)



b)

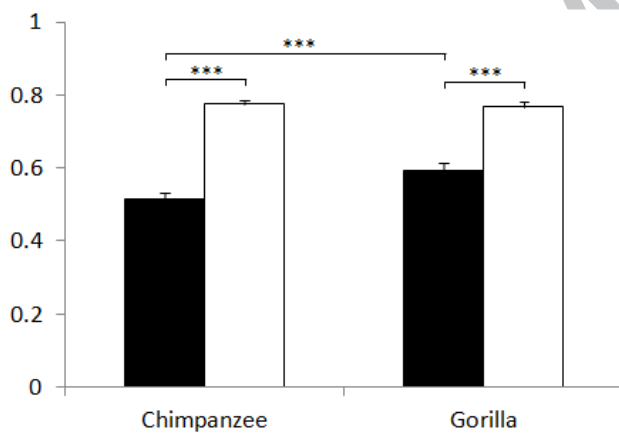


Figure 1: Adjusted probability (\pm SE) of right-hand use for each species. (a) Interactions with sensory modality: tactile, auditory, or visual gestures. (b) Interactions with Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field. Vertically striped bars: tactile 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.

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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
Gesture																		
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

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