

## Captive chimpanzees' manual laterality in tool use context: Influence of communication and of sociodemographic factors



Jacques Prieur<sup>a,\*</sup>, Simone Pika<sup>b</sup>, Catherine Blois-Heulin<sup>a</sup>, Stéphanie Barbu<sup>a</sup>

<sup>a</sup> *Ethos "Ethologie Animale et Humaine", Université de Rennes 1 – CNRS UMR 6552, Station Biologique de Paimpont, France*

<sup>b</sup> *Max Planck Institute for Evolutionary Anthropology, Department of Primatology, "Virtual Geesehouse", Deutscher Platz 6, 04103 Leipzig, Germany*

### ARTICLE INFO

#### Keywords:

Gestures

Hemispheric lateralization

Intraspecific communication

Object manipulations

*Pan troglodytes*

### ABSTRACT

Understanding variations of apes' laterality between activities is a central issue when investigating the evolutionary origins of human hemispheric specialization of manual functions and language. We assessed laterality of 39 chimpanzees in a non-communication action similar to termite fishing that we compared with data on five frequent conspecific-directed gestures involving a tool previously exploited in the same subjects. We evaluated, first, population-level manual laterality for tool-use in non-communication actions; second, the influence of sociodemographic factors (age, sex, group, and hierarchy) on manual laterality in both non-communication actions and gestures. No significant right-hand bias at the population level was found for non-communication tool use, contrary to our previous findings for gestures involving a tool. A multifactorial analysis revealed that hierarchy and age particularly modulated manual laterality. Dominants and immatures were more right-handed when using a tool in gestures than in non-communication actions. On the contrary, subordinates, adolescents, young and mature adults as well as males were more right-handed when using a tool in non-communication actions than in gestures. Our findings support the hypothesis that some primate species may have a specific left-hemisphere processing gestures distinct from the cerebral system processing non-communication manual actions and to partly support the tool use hypothesis.

### 1. Introduction

Laterality research evidences predominant involvement of humans' left-cerebral hemisphere in manipulations<sup>1</sup> (e.g. McManus, 1991) and communication by gestures<sup>2</sup> and spoken language (e.g. Kimura, 1973; Xu et al., 2009). However, several studies show ambiguous relationships between direction of handedness for manipulation and lateralisation of language (e.g. Pujol et al., 1999; Springer et al., 1999; Knecht et al., 2000; Josse and Tzourio-Mazoyer, 2004). For example, Knecht et al. (2000) showed that 96% right-handed individuals for manipulation<sup>3</sup> exhibited a left-brain hemisphere predominance for language in contrast to left-handed individuals of whom approximately 70% exhibited a left-brain hemisphere predominance for language and 30% a right-hemispheric or bilateral language organisation. The presence of this atypical association of language lateralisation and handedness questions whether particular manipulation functions reliably

predict hemispheric language lateralisation. If so, would complex manipulation actions associated with tool-use activities predict language lateralisation as authors have suspected for years (e.g. Greenfield, 1991)?

In fact, a growing body of literature supports the hypothesis of specific co-evolutionary relationships between language, gestures and tool-use<sup>4</sup> (e.g. see Stout and Chaminade, 2012 for review). According to this tool-use hypothesis, the strong predominance of right-hand use by humans would be a characteristic developed through tool use that was already presented by the common ancestor of humans and great apes (e.g. Greenfield, 1991; Breuer et al., 2005; Higuchi et al., 2009; Forrester et al., 2013). This hypothesis is supported by studies showing that children, chimpanzees and gorillas demonstrated population-level right-hand bias for unimanual actions directed towards an inanimate target (i.e. non-living functional object), but not for unimanual actions directed towards an animate target (i.e. social partner, self) (Forrester

\* Corresponding author at: JUMR 6552, Station Biologique, Université de Rennes 1, 35380 Paimpont, France.

E-mail address: [jac.prieur@yahoo.fr](mailto:jac.prieur@yahoo.fr) (J. Prieur).

<sup>1</sup> From here, we refer to manipulations as manual actions deprived of a communication function.

<sup>2</sup> From here, following the Pika's definition of gesture (Pika, 2008a,b), the term gesture is restricted to communication functions.

<sup>3</sup> Manual laterality assessed by the "Edinburgh handedness inventory" (Oldfield, 1971) considers a set of 10 items such as writing, drawing and the use of a knife.

<sup>4</sup> From here, we define tool use as the movement of a detached object that is used to change the location or condition of another object or organism (van Lawick-Goodall, 1970; Beck, 1980)

et al., 2011, 2012, 2013). This hypothesis is also supported by studies reporting that right-handed actions are associated to the left-cerebral hemisphere ability to deal with complex temporal sequences of motor activities required for tool making and use (Foucart et al., 2005; Weiss and Newport, 2006; Mercader et al., 2007). Language capacities would thus have emerged as an extension of this left cerebral hemisphere ability. This assumption is supported by brain imaging that evidences: first, that left-hemispheric anatomical specialisation of language areas have homologs in great apes (Gannon et al., 1998; Cantalupo and Hopkins, 2001; Hopkins and Nir, 2010) known to make and use tool (e.g. chimpanzees: McGrew and Marchant, 1992; bonobos: Kano, 1982; gorillas: Grueter et al., 2013; orangutans: Van Schaik et al., 2003); second, that asymmetries in the homologs of the human Broca's and Wernicke's areas are associated with chimpanzees' handedness for tool use (Hopkins et al., 2007); third that brain activity for perceiving language and using tools overlap in Broca's area (Higuchi et al., 2009).

Another useful approach to test the tool use hypothesis is to compare nonhuman primates' manual laterality of tool use in non-communication actions and in gestures. Adopting this comparative approach considering (1) our closest living relatives able to make and to use tools, chimpanzees (e.g. in the wild: McGrew and Marchant, 1992; in captivity: Paquette, 1992), and (2) real-life social interactions between conspecifics (i.e. conditions close to contexts in which natural selection acts) should provide valuable clues to enhance our understanding of co-evolutionary relationships between language, gestures and tool use. To date, existing studies concerning the effects of function (non-communication vs. communication) have compared laterality of tool use between manipulations and gestures (directed towards humans or both humans and conspecifics with pooled data). These studies evidenced greater right-hand use for gestures (i.e. FOOD BEG, POINTING, HAND SLAP, THROWING and/or a category of species-typical gestures combining THREAT, EXTEND ARM and HAND SLAP) than for manipulations (i.e. tool use, reaching and/or bimanual coordinated *tube task*) by chimpanzees (Hopkins et al., 2005a; Meguerditchian et al., 2010a), red-capped mangabeys and Campbell's monkeys (Maille et al., 2013), Tonkean macaques (Meunier et al., 2013), baboons (Meguerditchian and Vauclair, 2006; Meguerditchian et al., 2011; Meguerditchian and Vauclair, 2009; Meunier et al., 2012), and young children (e.g. Meunier et al., 2012). However, no study has yet compared manual laterality between non-communication and communication functions considering purely intraspecific gestural communication. Furthermore, no study has performed such comparisons considering tool-use activities in both functions. The present study aimed to tackle these issues.

Several factors known to modulate hand preference must be taken into account when comparing manual laterality between non-communication and communication functions in order to assess the effects particular to the function. Laterality in both functions can be modulated by various factors (e.g. see McGrew and Marchant, 1997; Meguerditchian et al. 2013 for reviews) such as age, sex, hierarchy, and group.<sup>5</sup> The potential effects of the demographic factors age and sex were the first to be investigated but the results were heterogeneous among studies.

Many studies show that direction and/or strength of hand preference for non-communication actions (e.g. chimpanzees: Boesch, 1991; bonobos: Chapelain and Hogervorst, 2009) and for gestures (e.g. chimpanzees: Hobaiter and Byrne, 2013; baboons: Meguerditchian and Vauclair, 2006), become more salient with age, suggesting that hand preference would be under the control of maturation and/or the result of practice, learning and/or experience. However, reports of age effects are not consistent either for non-communication actions (e.g.

chimpanzees: Hopkins, 1993; gorillas: Meguerditchian et al., 2010b) or for gestures (e.g. chimpanzees: Hopkins et al., 2005a; baboons: Meguerditchian and Vauclair, 2009), making it difficult to draw firm conclusions concerning the influence of age.

Sex can also influence manual laterality. Males' left-hand preference is greater than that of females for non-communication actions (e.g. chimpanzees: Byrne and Corp, 2003; De Brazza's monkeys: Schweitzer et al., 2007). To our knowledge, only two studies showed that sex influenced gestural laterality with however contradicting results: female chimpanzees tended to use their right hand more than males (Hopkins and Leavens, 1998) whereas female bonobos use their right hand less than males (Hopkins and de Waal, 1995). Nevertheless, other authors did not find influence of sex on manual laterality either for non-communication actions (e.g. see McGrew and Marchant, 1997 for review) or for gestures (e.g. chimpanzees: Hopkins et al., 2005a; Prieur et al., 2016; gorillas: Meguerditchian et al., 2010b), leaving open the issue of the influence of sex on laterality.

So far, only Prieur et al. (2016) investigated the influence of individuals' hierarchical status on manual laterality. They found that subordinate chimpanzee signallers overall used their right hand more to communicate with conspecifics than signallers belonging to higher hierarchical ranks. They hypothesized that stress produced by psychosocial factors would reduce subordinates' right-hemisphere activity (left-hand use) and thus increase the use of their right hand. Given the lack of studies, these issues need to be explored further.

In addition to individual characteristics such as age, sex and social status, the influence of belonging to a particular group and differences between groups have been investigated. Authors suggest several factors that could explain variations between social groups: first, genetic factors and/or social learning for laterality in non-communication actions (Lonsdorf and Hopkins, 2005; Hopkins, 2006); second, social stimulus/pressure for laterality in communication functions (e.g. Ghirlanda and Vallortigara, 2004; Ghirlanda et al., 2009; Versace and Vallortigara, 2015; Vallortigara and Versace, 2017). However, to our knowledge, no previous study reported an influence of the group on gestural laterality of captive non-human primates (e.g. chimpanzees for human-directed CLAPPING: Meguerditchian et al., 2012; baboons for HAND SLAP directed towards both humans and conspecifics (pooled data): Meguerditchian et al., 2011). Efforts to compare groups must continue to understand better the underlying mechanisms of population-level biases in laterality.

Discrepancies between the above-mentioned studies investigating the influence of age and sex on manual laterality may be the consequence of differences both between- and within-species related to the methodologies used to study manual asymmetries (e.g. see Cashmore et al., 2008 for review). For instance, we can quote disparities among manual activities considered (spontaneous actions or experimental tasks, function – for communication or not –, gestures directed towards humans and/or conspecifics) and among data collection and analyses (sample size, sociodemographic characteristics of the subjects, number of data points per subject, independence of data, statistical tests). Another reason for disparities is that these studies did not take into account simultaneously multiple potential influential factors (including sociodemographic factors) and their mutual interactions. However, this is essential to prevent biases leading to ambiguous findings and to assess the effects particular to the function (e.g. non-communication vs. communication). As far as we know, only Prieur et al. (2016) investigated the effects of sociodemographic factors on laterality using a comprehensive multifactorial approach. Furthermore, they took into account several narrow categories of age and hierarchical rank. Such comprehensive and fine-grained analysis is needed to better comprehend the effect particular to each modality of the considered variables.

The aim of the present study was to use such analysis to compare our closest living relatives', chimpanzees' (*Pan troglodytes*) manual laterality of tool use between non-communication and communication functions. We investigated the following questions and associated hypotheses:

<sup>5</sup> The term "group" meaning a set of interacting conspecifics that live in the same geographically delimited area during a substantial period of time perhaps a season or year (Wilson, 1975; Whitehead, 2008).

- (1) Knowing that chimpanzees were found to be right-lateralized for five frequently expressed conspecific-directed gestures involving the use of a tool (Prieur et al., 2016), is there also a manual laterality bias at the population level in chimpanzees when examining naturally occurring spontaneous daily non-communication tool-use actions using a stick to obtain an out-of-reach food reported in wild chimpanzees (e.g. Boesch and Boesch, 1990)? According to previous findings concerning chimpanzees' tool use involving the use of a stick (e.g. termite fishing; Bogart et al., 2012), we expected a marked laterality for tool use at the population-level (i.e. most subjects being lateralised) towards the left for the non-communication action.
- (2) Does manual laterality of tool use differ between non-communication and communication functions? If yes, what are the respective influences of the function and of the individuals' sociodemographic characteristics? To investigate this question, we compared manual laterality of tool use between both functions using a comprehensive approach considering simultaneously the effects of the functional and individual factors (non-communication, communication, age, sex, hierarchical rank, and group) and possible interactions between these factors. Based on the literature on chimpanzees (e.g. Meguerditchian and Vauclair, 2009; Hopkins et al., 2009; Prieur et al., 2016), we predicted, first, that communication would be more right-lateralized than non-communication action. Second, we expected modulation by age, sex, and hierarchy but not by group.

2. Methods

A full description of the subjects and of the observational and coding procedures for behaviours can be found in previous studies (Prieur, 2015; Prieur et al., 2016), and details are repeated here for the reader's convenience.

2.1. Subjects and settings

Thirty-nine chimpanzees were observed in three zoos: Leipzig Zoo (Germany), Beauval Zoo and La Palmyre Zoo (France). These zoos were chosen because they provide relatively similar living conditions for chimpanzees (i.e. large naturalistic enclosures and large social groups). Individual characteristics are presented in Table 1. Age categories were defined as: immatures (0–7 years old) (Goodall, 1986), adolescents (8–12 years old), young adults (13–20 years old), mature adults (21–35 years old), and elders (over 35 years old) (Hopkins and Leavens, 1998 for captive chimpanzees). For a detailed description of the housing conditions of the chimpanzees see Prieur (2015). As the study was non-invasive and involved only observations of animals in their enclosures, experimental permits or ethical approvals were not required.

2.2. Observation procedures

Observation data were collected by J.P. between July and December 2013 at the Wolfgang Köhler Primate Research Center at the Leipzig Zoo, at the Beauval Zooparc, and La Palmyre zoo, during respectively 333 h, 198 h and 174 h observation per group/zoo. Observation and coding procedures are presented below. Data were collected using the behaviour sampling rule “sampling all occurrences of some behaviours” with “continuous recording” for the recording rule (Altmann, 1974; Martin and Bateson, 1994). Observation data were collected in real time by using a stopwatch, binoculars, a paper sheet onto which data were recorded as well as a powerful pair of binoculars if necessary. Observations were made 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.

Data considered in the present study include:

Table 1 Individual characteristics of the study sample.

Name	Age	Sex	Social status	Zoo
<i>Elder (over 35 years)</i>				
Lavieil	54	F	S	Beauval
Joseph	38	M	D	Beauval
Robert	37	M	D	Leipzig
Fraukje	37	F	S	Leipzig
Charlotte	37	F	I	Beauval
Corrie	36	F	S	Leipzig
Ulla	36	F	S	Leipzig
<i>Mature adult (21–35 years)</i>				
Riet	35	F	D	Leipzig
Micheline	35	F	D	Beauval
Baraka	34	F	D	Beauval
Natascha	33	F	I	Leipzig
Dorien	32	F	I	Leipzig
Bono	31	F	I	Beauval
Lily	26	F	D	La Palmyre
Gypso	26	F	S	Beauval
Gamin	24	M	D	Beauval
Domi	24	F	I	Beauval
Julie	21	F	I	Beauval
<i>Young adult (13–20 years)</i>				
Christmas	20	F	I	La Palmyre
Sandra	20	F	I	Leipzig
Benji	19	M	D	La Palmyre
Isabelle	19	F	I	La Palmyre
Frodo	19	M	D	Leipzig
Swela	17	F	I	Leipzig
Melie	16	F	I	La Palmyre
<i>Adolescent (8–12 years)</i>				
Lome	12	M	D	Leipzig
Tai	11	F	I	Leipzig
Lulu	10	M	D	La Palmyre
Lobo	9	M	D	Leipzig
Kofi	8	M	D	Leipzig
Kara	8	F	S	Leipzig
<i>Immature (0–7 years)</i>				
Sangha	7	F	S	Beauval
Kelle	6	F	S	La Palmyre
Wamba	5	F	S	Beauval
Bangolo	4	M	S	Leipzig
Tumba	4	M	I	Beauval
Cheetah	3	F	S	La Palmyre
Lukombe	2	M	S	Beauval
Tsanaga	0.7	M	S	La Palmyre

F: Female; M: Male; D: Dominant; I: Intermediate; S: Subordinate.

- a new set of data for non-communication tool-use actions for 25 of these 39 subjects.
- a set of data for the five gestures with a communication tool previously exploited in these 39 subjects from the zoos of La Vallée, Apenheul, and Burgers (Prieur, 2015; Prieur et al., 2016) for which a new exploitation is made here in the framework of the statistical analysis.

2.3. Coding procedure for the non-communication tool-use actions

For comparison purpose with our previously exploited intraspecific gestural data (Prieur et al., 2016), naturally occurring spontaneous non-communication tool-use actions were recorded during captive chimpanzees' daily activities. These actions consist in using a stick to obtain an out-of-reach food. This tool manipulation requires precise motor actions, motor planning and hand to eye coordination. Such requirements are similar to those for termite fishing in the wild (e.g. chimpanzees: McGrew and Marchant, 1992) and for the tool use task designed by Hopkins et al. (2009) to simulate termite fishing in captive

chimpanzees.

In the three zoos, our chimpanzees were exposed on a daily basis to varying enrichment tools such as food boxes (raisin timbers, poking bins baited with pellets; for more information, see <http://wkprc.eva.mpg.de/english/files/enrichment.htm>), artificial concrete termite mounds baited with honey, and branches, enabling them to use sticks freely to obtain food. Data were also collected in other situations when the chimpanzees could only reach food with the use of a stick (e.g. food accidentally thrown by zookeepers and/or visitors in interstices at the edge of the enclosure or just out of reach near the edge). Following Hopkins et al.' (2009) procedure for data recording, we recorded the hand (left or right) used successfully by the subject (1) to insert a stick into a hole of the termite mound/an interstice at the edge of the enclosure and (2) to make contact using a stick with the food item just out of reach near the edge of the enclosure. Data recorded in both situations were pooled for analysis. For tool use requiring insertion of the stick, a subject would occasionally insert it with one hand and withdraw it with the other. In this case, the hand used to insert the stick was recorded as insertion demands more precise motor skills, motor planning, and hand-to-eye coordination. Not all the chimpanzees expressed non-communication tool-use actions: 25 (6 immatures, 6 adolescents, 4 young adults, 5 mature adults and 4 elders; 9 males and 16 females; 7 subjects from Beauval; 15 subjects from Leipzig and 3 subjects from La Palmyre) of the 39 studied chimpanzees performed a sufficient number of these behaviours to be used for subsequent statistical analyses.

#### 2.4. Coding procedure for conspecific-directed gestures involving a communication tool

In parallel with observations of spontaneous non-communication tool-use actions, five spontaneous gestures performed by signallers directed towards a given conspecific involving a communication tool were also recorded.<sup>6</sup> Data related to these five frequently expressed conspecific-directed gestures were subject to a first analysis (Prieur, 2015; Prieur et al., 2016). Only dyadic interactions between conspecifics were taken into account. For each interaction, we recorded (1) type of gesture, (2) hand (left or right) used by the signaller to communicate with a particular recipient (i.e. the hand that held the communication tool), and (3) identity of the signaller (i.e. its socio-demographic characteristics).

Based on Pika and Bugnyar's (2011) definition of gesture, only behaviours that met the following criteria 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 and de Waal, 2007), and (d) elicited a voluntary response by recipients. Among all the conspecific-directed gestures observed in the three study groups of chimpanzees, we focused on five particular gestures that involved the use of a communication tool and that were expressed sufficiently frequently to enable comparisons with non-communication tool-use actions. We also observed other gestures involving a tool previously described for wild chimpanzees (Nishida et al., 2010), but extremely rarely. These five conspecific-directed gestures were classified based on previous descriptions of such gestures in the literature (when necessary anatomical elements or precisions were added). They are listed and described in Appendix Table A1.

#### 2.5. Data requirements and independence for non-communication actions and gestures recorded

The present study focused on the hand used by the subject to manipulate a stick to obtain out-of-reach food and to perform conspecific-

directed gestures with an object used as a communication tool. We recorded hand use only when both the initiator's hands were free and placed symmetrically with respect to its body midline before performing the action (non-communication or communication), without any external factors that could potentially affect hand laterality (e.g. proximity of a wall). We recorded data only for single actions and action bouts (e.g. Marchant and McGrew, 1991). For each bout, only the first manual action was considered. To ensure statistical independence of data (e.g. Hopkins and de Waal, 1995), an action was recorded as a new action event when a change in hand activity lasted more than three seconds (e.g. the signaller ceased to communicate by leaving the location to search for food sources during more than 3 s).

#### 2.6. Identification of hierarchical rank

In addition to individual demographic characteristics (age, sex, zoo), we considered social status. Hierarchical ranks were determined previously (Prieur et al., 2016). Details are repeated here for the reader's convenience.

Hierarchical ranks were based on the analysis of agonistic interactions (Pollick and de Waal, 2007) within dyads when aggressor and recipient of the threat were clearly identified (Langbein and Puppe, 2004). Following the coding procedure for conspecific-directed gestures involving a communication tool previously described, we recorded every dyadic agonistic interaction that occurred during our observation time (4334 in all). These agonistic interactions include for example the following intentional signals: PUNCH, HAND SLAP, HIT WITH BRANCH, and GRAB BODY.

We organized these interactions into sociomatrices from which we calculated Kendall's coefficient of linearity  $K$ , Landau's linearity index  $h$  and the index of linearity  $h'$  using MatMan 1.1 (Noldus Information Technology, Wageningen, Netherlands) (de Vries, 1995; de Vries et al., 2006). The software analysis assigns a rank from 1 (the most dominant) to  $N$  (the most subordinate) to each of the  $N$  individuals of one zoo. Three categories of hierarchical rank were considered: "Subordinate", "Intermediate", and "Dominant" (Beauval: 5 subordinates, 5 intermediates and 4 dominants; Leipzig: 5 subordinates, 5 intermediates and 6 dominants; Palmyre: 3 subordinates, 3 intermediates and 3 dominants).

#### 2.7. Statistical analyses

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

##### 2.7.1. Descriptive statistics of laterality at the individual and population level

To enable subsequent statistical analyses using the two-tailed binomial test (Siegel and Castellan, 1988), we only used data for behaviours that had been performed at least six times each by at least six individuals (e.g. Prieur et al., 2016).

Individual-level bias was assessed for each individual and each behaviour using the binomial test on the number of responses performed by the individual with its left or right hand. A subject exhibiting a significant bias (respectively no bias) was categorised as lateralised (respectively non-lateralised). For each individual, the direction of asymmetry was evaluated 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). The strength of individual hand preference was measured by the absolute value of the  $HI$  (ABS $HI$ ). This procedure is similar to that used by previous authors (e.g. Harris and Carlson, 1993).

Following previous authors (e.g. Hopkins et al., 2005a), "population level" refers to all the individuals of the three groups/zoos studied. Population-level bias in the number of lateralised and non-lateralised

<sup>6</sup> The gesture characteristic – use of a communication tool (with or without object) – was defined following a pilot study (see Prieur, 2015 for details) so that this parameter was not recorded during the data collection (on-site at the zoo).



individuals was assessed for each behaviour using the binomial test. For each behaviour when at least six subjects were lateralised, we assessed population-level bias in the number of right-handers and left-handers using the binomial test. As Bourne (2008) remarked “measuring handedness on a continuum, rather than dichotomously, has significant advantages as it is able to potentially reveal more subtle relationships between handedness and cerebral lateralisation” p. 350. To better understand handedness and for comparisons purposes with recent studies (e.g. McGrew and Marchant, 1997; Corballis, 2002; Hopkins et al., 2012; Prieur, 2015) we considered laterality on a continuum to evaluate bias in hand use at the population level. We assessed this bias by a one-sample two-tailed Student’s *t*-test on the HI values of all the individuals when the distribution of HI data was normal (Shapiro-Wilk normality test). Authors have suggested that sample size can influence conclusions concerning direction and strength of laterality (McGrew and Marchant, 1997; Palmer, 2002). Therefore, the potential effect of the number of data points per individual on the direction (HI) and strength (ABSHI) of laterality was assessed using the Spearman correlation test.

2.7.2. Generalised linear mixed model analysis considering multiple influential factors

To assess differences in hand use between tool-use activities in gestures and in non-communication actions (i.e. gestures involving a tool noted “C Tool use” vs. non-communication tool-use actions noted “NC Tool use”) by taking into account simultaneously all possible interactions with the individuals’ sociodemographic characteristics (i.e. age, sex, hierarchical rank, zoo), we evaluated the effects of these functional and individual variables on laterality using a generalised linear mixed model (GLMM) for binary data (logistic regression) with hand use as the dependent variable, following the Prieur et al.’s (2016) procedure. Initiators’ identity was considered a random variable to prevent pseudo-replication due to repeated observations (Waller et al., 2013) (see Table 2 for a descriptive summary of dependent, fixed and random variables). To avoid numerical instabilities in the GLMM procedure, the five conspecific-directed gestures involving a communication tool (DRAG OBJECT, PUT OBJECT ON HEAD/BACK, SHAKE OBJECT, THROW OBJECT and HIT WITH OBJECT) were regrouped in one category noted “C Tool use”. This regrouping of four visual gestures and one tactile gesture was justified by results showing that sensory modality did not modulate laterality of gestures involving use of a communication tool (Prieur et al., 2016). Furthermore, we checked every result provided by the GLMM analysis to detect potential outlier in the estimate (difference between Least Square means (LSmeans)), the

**Table 2**  
Generalized linear mixed model with the dependent, fixed and random variables, their type and associated levels.

Name	Type
<i>Dependent variable</i>	
Hand use	Dichotomous (Left/Right)
<i>Fixed variables</i>	
Initiator’s age class	Ordinal (Immature/Adolescent/Young adult/Mature adult/Elder)
Initiator’s sex	Dichotomous (Female/Male)
Initiator’s hierarchical rank	Ordinal (Dominant/Intermediate/Subordinate)
Initiator’s zoo	Nominal (Beauval/Leipzig/Palmyre)
Tool-use activity	Dichotomous (C Tool use/NC Tool use)
<i>Random variable</i>	
Initiator’s identity	Nominal

C Tool use: Communication tool use; NC Tool use: Non-communication tool use.

standard error of the difference, the z.ratio (ratio of the estimate to its standard error) (Appendix Tables A5–A8) as well as the confidence intervals associated with the adjusted probabilities of right-hand use and the standard error of the adjusted probability (Appendix Table A9). All possible interactions between fixed variables were included at the beginning of the iterative model selection.

For the GLMM analyses, we used the ‘glmer’ function [‘lme4’ package (Bates et al., 2014)]. We selected the best model as the one with the lowest Akaike’s information criterion (AIC). We checked visually 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 and 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 (from here, noted “Tukey test”) to prevent Type I errors and differences were calculated between LSmeans (lsmeans package).

3. Results

3.1. Manual laterality in non-communication tool use at the population level (question 1)

We recorded 1689 occurrences of non-communication tool-use actions for 25 chimpanzees. After having applied the statistical criterion required for binomial tests (Siegel and Castellan, 1988), 1678 occurrences of non-communication tool-use actions for 19 chimpanzees were retained for the following analysis of manual laterality at the population level. The mean number of occurrences per individual was 88.32 for the non-communication tool-use actions (min = 14, max = 278; SD = 72.29) (Appendix Table A2).

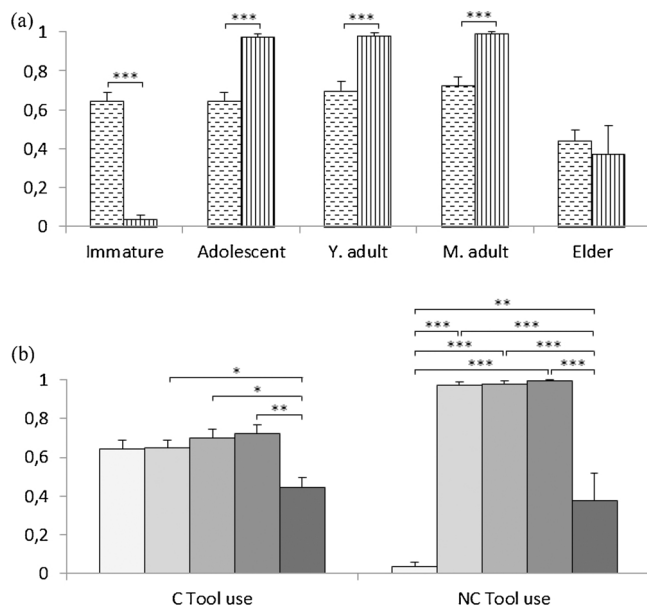
The study of manual laterality of tool use in non-communication actions at the population level showed no statistically significant differences between the numbers of non-lateralised subjects (6) and lateralised subjects (13) (binomial test: *P* = 0.167). The associated average percentage of non-lateralised individuals was 31.58%. Moreover, no statistically significant differences between the numbers of right-handed subjects (9) and left-handed subjects (4) was found for non-communication tool-use actions (binomial test: *P* = 0.267). Considering laterality on a continuum, rather than dichotomously, no population-level bias in the direction of hand preference was found for non-communication tool-use actions (Mean HI = 0.22; Mean ABSHI = 0.54), (one-sample two-tailed *t*-test, *P* = 0.130).

For comparison purpose, Appendix Table A2 presents the analyses of manual laterality at the population level for the five conspecific-directed gestures involving the use of a tool previously exploited (Prieur et al., 2016).

No significant effect of number of data points per individual on the HI and ABSHI values for non-communication tool-use actions as well as for each of the five conspecific-directed gestures involving a tool was found (Spearman correlation test, Appendix Table A3).

3.2. Manual laterality in tool use in non-communication and communication functions: modulation by sociodemographic factors (question 2)

To assess whether, and how, function – communication vs. non-communication – impacted subjects’ laterality in tool-use activities according to the subjects’ sociodemographic characteristics, we carried out a GLMM analysis taking into account not only all the 1689 occurrences of non-communication tool-use actions for 25 chimpanzees presented above, but also all the 6647 occurrences of gestures involving a communication tool for 39 chimpanzees (data previously recorded and exploited by Prieur et al., 2016). The associated mean numbers of



**Fig. 1.** Adjusted probability ( $\pm$  SE) of right-hand use for communication and non-communication tool-use activities. Interaction with initiators' age class. (a) between tool-use activities: dashed horizontal bars: communication tool use, vertically striped bars: non-communication tool use. (b) within tool-use activities: gradual range of grey bars: age classes from light grey (Immature) to dark grey (Elder). Tukey test: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

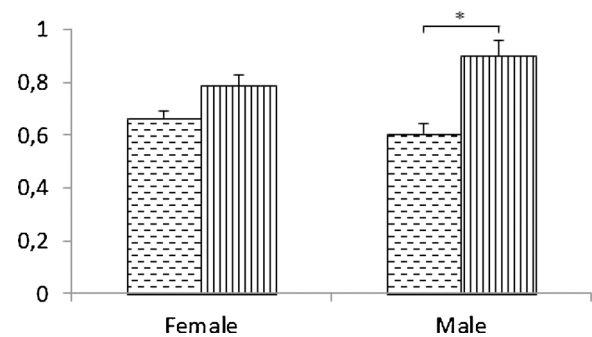
occurrences per subject were 67.60 for the non-communication tool-use actions (minimum = 1, maximum = 277; SD = 72.72) and 170.46 for the five gestures (minimum = 1, maximum = 841; SD = 234.40). The analysis of deviance results corresponding to the best GLMM model is displayed in Appendix Table A4. Significance of fixed variables (considered separately) was not accounted for since every variable was involved in significant interactions with other variables. Only significant interactions were thus considered. The results of post-hoc multiple comparisons are in Appendix Tables A5–A8. For clarity, significant and trend p-values are mentioned in the text below whereas all p-values can be found in Tables A5–A8. Appendix Table A9 presents the confidence intervals associated with the adjusted probabilities of right-hand use for each significant interaction.

### 3.2.1. Influence of communication in tool-use activity in relation to subjects' age class

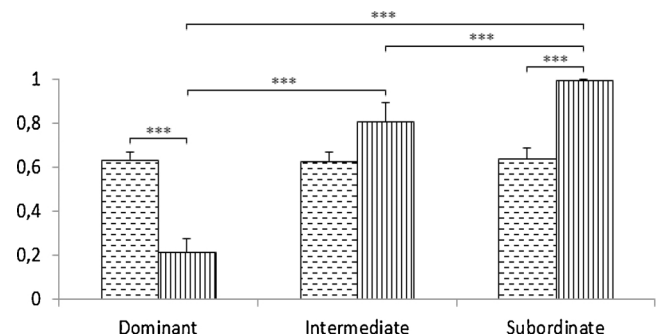
Laterality patterns differed between age classes (Fig. 1a). Adolescents, young and mature adults were more right-handed when using a tool in non-communication actions than in gestures (Tukey test: adolescents:  $P < 0.0001$ ; young adults:  $P < 0.0001$ ; mature adults:  $P = 0.0003$ ). The opposite pattern was found for immatures who were more right-handed for gestures than for non-communication actions ( $P < 0.0001$ ). No significant communication effect was found for elders. Communication and non-communication tool use differed significantly between age classes (Fig. 1b). Elders were less right-handed than all the younger age classes for gestures; this difference was significant for adolescents, young and mature adults (adolescents:  $P = 0.035$ ; young adults:  $P = 0.017$ ; mature adults:  $P = 0.002$ ), but not for immatures. No significant differences appeared between the other age classes. Elders and immatures were significantly less right-handed than adolescents, young and mature adults for non-communication actions (all  $P < 0.0001$ ). Immatures were less right-handed than elders ( $P = 0.006$ ). Levels of laterality for non-communication actions for the other age classes, adolescents, young and mature adults, were similar.

### 3.2.2. Influence of communication in tool-use activity in relation to sex

Males' and females' patterns of laterality were similar (Fig. 2).



**Fig. 2.** Adjusted probability ( $\pm$  SE) of right-hand use for communication and non-communication tool-use activities. Interaction with initiators' sex. Dashed horizontal bars: communication tool use. Vertically striped bars: non-communication tool use. Tukey test: \* $P < 0.05$ .



**Fig. 3.** Adjusted probability ( $\pm$  SE) of right-hand use for communication and non-communication tool-use activities. Interaction with initiators' hierarchical rank. Dashed horizontal bars: communication tool use. Vertically striped bars: non-communication tool use. Tukey test: \*\*\* $P < 0.001$ .

initiators but not females were significantly more right-handed when using a tool in non-communication actions than in gestures (Tukey test: male:  $P = 0.039$ ; female:  $P = 0.079$ ). No evidence of significant between-sex differences was found whatever the function.

### 3.2.3. Influence of communication in tool-use activity in relation to hierarchical rank

Patterns of laterality differed with social status (Fig. 3): dominants were more right-handed when using a tool in gestures than in non-communication actions (Tukey test:  $P < 0.0001$ ) whereas subordinates were more right-handed for non-communication actions than for gestures ( $P < 0.0001$ ). No communication effects of tool-use activity were evidenced for intermediate initiators. Between-rank comparisons revealed no evidence of a significant influence of initiators' hierarchical status on initiators' right-hand use for gestural communication; all ranks had very similar levels of laterality for gestures involving a communication tool. However, right-hand use for non-communication actions increased significantly with decreasing hierarchical rank: dominants were less right-handed than intermediates ( $P < 0.0001$ ) who were less right-handed than subordinates ( $P < 0.0001$ ).

### 3.2.4. Influence of communication in tool-use activity in relation to group (zoo)

There was no evidence of significant communication effects on tool-use activity whatever the zoo. Comparisons between the three zoos evidenced no influence of zoo whatever the function. In all, these results indicated that the influence of group/zoo was limited.

## 4. Discussion

Our study compared chimpanzees' manual laterality for tool use in non-communication and communication functions. We questioned first, whether manual laterality was observed at the population level for non-communication tool-use actions; second, whether and how manual laterality of tool use in both functions was modulated by individuals' sociodemographic characteristics. Considering laterality on a continuum, we did not find a population-level right-hand use bias for non-communication tool-use actions, contrary to what we found for each of the five conspecific-directed gestures involving a tool considered in our previous studies (Prieur et al., 2016). Moreover, our multivariate study showed that manual laterality of tool-use was influenced by the effects of the functional and individual factors as well as their mutual intertwinement. Laterality of dominant and immature initiators was directed more to the right for gestures than for non-communication actions. On the contrary, subordinates, adolescents, young and mature adults as well as males were more right-handed for non-communication actions than for gestures.

### 4.1. Manual laterality in non-communication tool use at the population level (question 1)

We did not find evidence of a population-level bias for the non-communication tool-use actions. Our results are consistent with reports of captive chimpanzees performing a tool-use task designed to simulate termite fishing (Hopkins et al., 2009). Conversely, studies on laterality in termite fishing by two wild chimpanzee communities revealed a left-hand bias at the population level (Gombe: e.g. McGrew and Marchant, 1992; Fongoli: Bogart et al., 2012). The difference in hand preference between the present study and these studies of wild chimpanzees could be due to a "difference in haptic and sensory requirements during insertion and extraction" (Hopkins et al., 2009; p. 9) between our non-communication tool-use actions and termite fishing in the wild. This divergence of results may also be the consequence of genetic factors and/or social learning on laterality suggested to explain task-specific variation in direction of laterality between groups of wild chimpanzees in tool-use actions (Lonsdorf and Hopkins, 2005). However, our results concerning the three study groups did not support an effect of genetic factors and/or social learning on laterality. Indeed, we did not find any differences of the laterality patterns between the three groups either for non-communication tool-use actions or for gestures. However, this finding must be considered with caution because of uneven number of individuals from each study group. An absence of group effect on manual laterality in both functions was also found in previous studies of captive chimpanzees (e.g. for the *tube task*: Hopkins et al., 2004; for *THROWING*: Hopkins et al., 2005a).

For communication function involving the use of a tool, a right-hand bias at the population level was found by previous studies on chimpanzees' laterality in gestures directed towards conspecifics (e.g. for *DRAG OBJECT*, *PUT OBJECT ON HEAD/BACK*, *SHAKE OBJECT*, *THROW OBJECT* and *HIT WITH OBJECT*: Prieur et al., 2016; for a category of object-manipulation gestures combining *OBJECT SHAKE* and *OBJECT MOVE*: Hobaiter and Byrne, 2013) and in gestures directed towards humans or both humans and conspecifics (for *THROWING*: Hopkins et al., 1993, 2005a; Hopkins, 2006).

To sum up, the above findings on chimpanzees' laterality for tool-use in non-communication actions and in gestures support previous studies in favour of a predominant implication of the left-cerebral hemisphere in the gestural communication system of some non-human primates (e.g. Hopkins et al., 2012; Meguerditchian et al., 2013). However, this conclusion must be considered with caution, as manual laterality for tool use in both functions was modulated differently in relation to sociodemographic factors.

### 4.2. Manual laterality in tool use in non-communication and communication functions: modulation by sociodemographic factors (question 2)

As far as we know, the present study is the first to compare non-human primates' manual laterality between non-communication and communication functions focusing on tool-use activities. Our results concerning the effects related to the function (non-communication and communication) can thus only be discussed in relation to studies comparing laterality for object manipulations and gestures without a tool. Furthermore, these studies considered gestures directed towards humans or both humans and conspecifics contrary to our study which only considered intraspecific communication. To discuss our results concerning the effect particular to the function (non-communication and communication) and compare them with these studies, the respective influences of sociodemographic factors on manual laterality of tool use in both functions must be analyzed first.

#### 4.2.1. Influence of initiator's hierarchical rank

We found evidence for the first time, of an influence of hierarchical status on manual laterality in non-communication actions: dominants were less right-handed than intermediates who were less right-handed than subordinates. Chimpanzees are very competitive over food resources (e.g. Hare, 2001; Wittig and Boesch, 2003). Our subjects were mostly foraging in relative close proximity and this elicited feeding competition among conspecifics, particularly when a tool was used to obtain out-of-reach desirable food (i.e. in non-communication actions). We assumed that the observed increase in right-hand use with decreasing hierarchical rank in the context of food access could be associated with a higher level of psychosocial stress. This hypothesis is supported by several studies showing that low-ranking social animals usually maintain a higher level of glucocorticoids (i.e. stress hormone) than high-ranking subjects (e.g. Creel, 2001; Markham et al., 2014). Furthermore, captivity could enhance psychosocial stress (Creel et al., 1996; Muller and Wrangham, 2004). Authors have reported that steroid hormones can modulate differently functional hemispheric asymmetries in relation to the developmental stage as well as nature and duration of the stressor (e.g. acute vs. chronic stress), yielding heterogeneous results among laterality studies (e.g. see Ocklenburg et al., 2016 for a review concerning stress-induced changes of laterality in various species). Several authors showed a greater involvement of the right hemisphere/left body side in acute and chronic stress (e.g. see Rogers et al., 2013 for a full discussion of the role of stress and right hemispheric functions in various species). However, such right hemispheric predominance in stress conditions has not been consistently found across studies and some authors have hypothesized that stress would induce a population-level right-side bias in several non-human animals (chimpanzees: Prieur et al., 2016; gorillas: Prieur, 2015; rats: e.g. Alonso et al., 1991; anoles: Deckel, 1998). This hypothesis is supported by Rohlf's and Ramirez's (2006) review of humans' asymmetries mentioning that stress could induce several neurochemical changes (e.g. increase of dopamine: Bertolucci-D'Angio et al., 1991) causing structural and functional alterations in the right hemisphere (Joseph, 1994; Schore, 1997; Ben-Shachar et al., 1995). Probably these alterations in the right hemisphere could inhibit its activity and thus consequently reduce use of left hand. This would result indirectly in an increase of right-hand use as observed during stress in subordinate and, to a lesser extent, intermediate chimpanzees.

On the contrary, we found no hierarchical rank effect for gestures involving a tool. Except *HIT WITH OBJECT*, the other four gestures studied are visual gestures. Our results are thus coherent with our previous study reporting the absence of a hierarchical rank effect for visual gestures but not for tactile gestures (Prieur et al., 2016). Laterality of tactile gestures could be affected by psychosocial stress potentially because these gestures imply close proximity between partners. On the contrary, gestures involving the use of a communication tool

(mainly visual gestures) were expressed generally when inter-individual distances were relatively greater than for tactile gestures. Therefore, we hypothesized that they would be potentially less associated with psychosocial stress. These differences would explain the absence of effects of hierarchical rank on laterality for gestures involving a tool.

#### 4.2.2. Influence of initiator's age class

Our comparisons between age classes for non-communication actions and gestures indicated that elders were less right-handed than adolescents, young and mature adults. Such age-related asymmetry reduction is consistent with the HAROLD model, a cognitive neuroscience model, stating that prefrontal activity during cognitive performances tends to be less lateralized in older adults than in younger adults (e.g. Cabeza, 2002). This model is supported by functional and behavioral evidence in the domains of episodic memory retrieval (e.g. Cabeza et al., 1997), working memory (e.g. Reuter-Lorenz et al., 2000), perception (e.g. Grady et al., 2000), and inhibitory control (e.g. Nielson et al., 2002). More recently, behavioral laterality studies have provided further support to the HAROLD model by showing a decrease of right-hand use in 60 humans for non-communication actions (Kalisch et al., 2006) and in 39 chimpanzees for gestural communication (Prieur et al., 2016). Potential causes might be related to (1) physical limitations and lesser activity (already documented for humans: Hughes et al., 1997; Schut, 1998; Ranganathan et al., 2001) that would decrease right-hand practice-based performance and/or (2) lower elder subjects' sociability (personal observations). Ultimately, these possible causes could produce a shift towards ambidexterity with aging. As far as we know, this is the first evidence of a possible effect of senescence on primates' manual laterality for both non-communication actions and gestures.

Immatures were less right-handed than adolescents, young and mature adults and elders for non-communication actions. This move towards the right with age until the shift at an older age of tool-use actions is coherent with previous reports concerning non-human primates (chimpanzees: Boesch, 1991; capuchin monkeys: Westergaard and Suomi, 1993, 1994) and humans (e.g. see Schaafsma et al. 2009 for review). Immatures' low-level of right-hand use may be due to a lack of maturation and/or practice, learning and experience (e.g. see McGrew and Marchant, 1997 for review). However, five of our six immatures were subordinates. As most immatures were subordinates, we expected them to be particularly right-handed when using a tool to obtain food because of psychosocial stress as hypothesized previously. However, this was not the case possibly because immature chimpanzees' motor and cognitive abilities that control stress would be less developed and thus less effective than those of older subjects. This assumption is supported by the fact that humans' neural circuits that deal with stress are particularly plastic during early childhood, experience shaping them progressively (De Bellis, 2005). Moreover, the fact that the potential lower efficacy of immatures' motor and cognitive abilities to control stress could be combined with an effect of the haptic demand of the task (particularly pronounced for subordinates as developed below) might explain their particularly low level of right-hand use for non-communication tool-use actions. Indeed, because dominants were generally the first individuals of the group to obtain access to a palatable food source, they obtained the major part of the food more easily than lower-ranking subjects, especially subordinates (including immatures) who had to perform more controlled and finer haptic manipulations of the tool to extract the rest of the food (personal observations). The particular low level of right-hand use by immatures for non-communication tool use could be explained by the greater involvement of the right-cerebral hemisphere (i.e. left hand) for the processing of haptic information during visual-tactile tasks (capuchin monkeys: Lacreuse and Fragaszy, 1999; Spinozzi and Cacchiarelli, 2000).

Immatures' laterality pattern for gestures involving a tool did not differ statistically from that of older subjects. Our results showed an

absence of differences between all age classes except elders for gestures. This supports the only other study of age effects on gestural laterality involving use of a tool (Hopkins et al., 2005b).

#### 4.2.3. Influence of initiator's sex

Between-sex comparisons did not reveal any evidence of sex differences in initiators' right-hand use for either non-communication actions or gestures. This is in accordance with most studies that did not find a sex effect on manual laterality for both functions (e.g. captive chimpanzees: Hopkins et al., 2004, 2005b; see also McGrew and Marchant, 1997 for review). However, other studies evidenced that females were more right-handed than males for termite fishing (e.g. chimpanzees: Hopkins et al., 2009) as well as for some gestures (see Meguerditchian et al., 2013 for review).

#### 4.2.4. Influence of function: non-communication versus communication

We found that dominant and immature initiators were more right-handed when using a tool in gestures than in non-communication actions. The contrary was found for subordinates, adolescents, young and mature adults as well as males. However, no differences were evidenced for intermediates, elders, females or groups/zoos.

Dominants may be less subject to psychosocial stress related to food access than lower-ranking subjects (i.e. intermediates and subordinates). Therefore, we assumed that the difference observed for dominants would represent at the best the effect of the function (i.e. gestures with a tool elicit greater right-hand use than manipulations with a tool). The hypothesized effect of psychosocial stress on subordinates' right hand use would lead to a converse effect (i.e. right hand used more for manipulations than for gestures with a tool).

The difference observed for immatures, predominantly subordinates, concerning function could be explained by (1) a weaker effect of psychosocial stress possibly due to less effective motor and cognitive abilities and (2) the specific haptic demands of the tool task associated with lower-ranking individuals. Only one of the 15 adolescents, young and mature adults was a subordinate. Their greater right-hand use observed for non-communication actions than for gestures may be attributed to the absence of haptic constraints combined with age-related experience known to reinforce right direction in hand preference (e.g. Boesch, 1991).

Males' but not females' right-hand use was greater for non-communication actions than for gestures. Two non-exclusive reasons could explain differences of function effect between males and females. First, they could be the consequence of differences in practice and/or learning, factors known to influence non-human primates' manual laterality (e.g. Warren, 1980). On average, males manipulated tools 1.7 times more often during our observations than did females. We hypothesize that our males were more experienced than the females for non-communication actions, either by having started to perform earlier than females and/or having performed them more frequently. This hypothesis is supported by a report showing that cats shifted paw use to the right after practice of a visual motor task (Lorincz and Fabre-Thorpe, 1996). Second, the potential influence of hormones on laterality has rarely been studied in non-human primates but studies suggested that circulating hormones (including testosterone and cortisol) could affect rhesus monkeys' laterality by increasing or decreasing its strength (Drea et al., 1995; Westergaard et al., 2000) or modifying its direction (Westergaard and Lussier, 1999; Westergaard et al., 2000, 2003). Further research is required to explore the influence of sex on manual laterality and its determinants.

As previously mentioned, existing studies comparing manual laterality between communication and non-communication functions did not consider tool-use activities in both functions and did not consider only gestures directed towards conspecifics (e.g. Hopkins et al., 2005a; Meguerditchian and Vauclair, 2006). Consequently, their results cannot be rigorously compared to ours. Nevertheless, a link is possible. Their common conclusion (i.e. greater right-hand use for communication than for non-communication) could be related to the methodology used in their non-human



primates’ studies, when examined in the light of our results concerning hierarchical effect on laterality of tool-use manipulations. First, equitable availability of the test apparatus to all of the individuals was probably not completely respected, namely higher-ranking individuals (dominants and intermediates) could have been overrepresented. In fact, their subjects were either mainly dominants when access to the apparatus was free or individuals isolated from dominant conspecifics before being tested. In the first case, it would be the consequence of a significant advantage in food access for higher-ranking individuals that would induce subordinates to renounce trying to participate in experiments in the presence of dominants. In the second case the number of intermediates tested (less likely to be stressed as isolated from dominants) was larger than the number of subordinates because subordinates are very often reluctant to leave their social group to be isolated and to participate in experiments (personal observation). When lower-ranking subjects were tested after physical isolation from higher-ranking conspecifics, they were probably less stressed psychosocially than when they were not isolated (as in our study). They would thus have used less their right hand for non-communication actions.

Our results concerning the function effect for dominants who were potentially free from psychosocial stress and haptic constraints of tool use to obtain food support the hypothesis that some non-human primate species and young children may have a specific left-hemisphere processing of gestural communication distinct from the cerebral system involved in non-communication manual actions (e.g. Meguerditchian and Vauclair, 2009). This hypothesis is in agreement with magnetic resonance imaging studies of chimpanzees (e.g. Hopkins and Cantalupo, 2004; Meguerditchian et al., 2012).

**5. Conclusion**

First, our study did not reveal any population-level right-hand use bias for non-communication tool-use actions, contrary to our previous findings for gestures involving a tool (Prieur et al., 2016). Second, our study showed the intertwining effects of the tool-use context and sociodemographic factors on chimpanzees’ manual laterality. Their laterality for tool use was not only influenced by the type of activity (communication or manipulation) but also modulated by individual characteristics, mainly hierarchy, age and, to a lesser extent, sex. Third, our findings concerning dominant chimpanzees and our previous findings concerning chimpanzees’ intraspecific gestural laterality (Prieur et al., 2016) lead us to hypothesize that primates’ right-side predominance for gestures without a tool (involving only communication components) would be greater than for gestures with a tool (involving both communication and manipulation components) that would be in turn greater than for non-communication actions. These

**Appendix A**

**Table A1**  
Gestural repertoire and detailed description.

Gesture	Description	Reference
DRAG OBJECT	Subject pulls an object (e.g. branch) on the ground with one hand towards another subject	Nishida et al. (2010)
PUT OBJECT ON HEAD/BACK *	Subject places an object (e.g. branch) on its head/back with one hand	Nishida et al. (2010)
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 (1998)
THROW OBJECT *	Subject sends an object (e.g. branch) through the air with one hand towards another subject	Hohmann and Fruth (2003)
HIT WITH OBJECT *	Subject clubs another subject with object (e.g. branch) held in one hand	Nishida et al. (2010)

Conspecific-directed gestures are organised by sensory modality (four visual gestures then one tactile gesture) and for each sensory modality listed by alphabetic order. Repertoire and details description of gestures were taken from a previous publication (Prieur et al., 2016). Gestures marked \* are followed by descriptions inspired from the mentioned reference(s); they are labelled differently because precisions based on personal observations have been added.

findings support the hypothesis that manipulation and communication components would not share the same lateralised cerebral system in some primates. Although the use of a tool for non-communication actions elicited strong laterality (direction and particularly strength), we did not evidence a related population-level right-hand bias. Therefore, our overall results partly support the “tool-use hypothesis” (e.g. Greenfield, 1991; Higuchi et al., 2009; Forrester et al., 2013) as the complex tool-use temporal sequences requiring high sensorimotor involvement for both functions induce a strong right-hand use. However, our conclusions must be considered with caution. Indeed, it would be necessary to test these three hypotheses on other naturally occurring spontaneous tool-use actions such as wadge-dipping/leaf-sponging (e.g. Boesch, 1991; Lonsdorf and Hopkins, 2005). Further studies are thus necessary to confirm whether tool use could have been an essential selective pressure determining the emergence of the two most pronounced manifestations of humans’ hemispheric specialisation that are right-handedness for manipulation and left-hemispheric specialisation for language. In addition, our study underlines the need to explore laterality considering real-life situations and potentially influential factors to ensure a relevant and reliable comparative approach between studies and species.

**Disclosure Statement**

The authors declare that they have no conflict of interest.

**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 and the zoo of La Palmyre, France and particularly Daniel Hanus, Josep Call, Aude Desmoulins, Romain Potier, Florence Perroux and Thierry Petit for allowing us to study their chimpanzee groups as well as for their friendliness and helpfulness. We are also indebted to Amandine Chapelain for her advice about the design of the observation protocol and to Russell Lenth, Maxime Hervé and Peter Green for their statistical advice as well as to Ann Cloarec for correcting the English.

**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 ([www.humboldt.de](http://www.humboldt.de)) to S.P.

**Table A2**  
Characteristics, descriptive statistics and analyses for each manual activity.

Manual activity	Sensory modality	N total	Data points total	N analysed	Data points analyzed	Non-lateralized	B test Lat. vs. Non-lat.	LH
<i>Conspicuous-directed gesture</i>								
DRAG OBJECT	Visual	22	510	13	488	11	<b>0.023</b>	0
PUT OBJECT ON HEAD/BACK	Visual	20	396	11	386	6	1	0
SHAKE OBJECT	Visual	39	5097	38	5096	18	0.871	1
THROW OBJECT	Visual	26	376	12	348	5	0.774	1
HIT WITH OBJECT	Tactile	23	268	12	249	7	0.774	0
<i>Non-communication tool-use actions</i>								
	–	25	1689	19	1678	6	0.167	4

Manual activity	RH	B test LH vs. RH	Mean HI	Shapiro test	t-test	Mean ABSHI
<i>Conspicuous-directed gesture</i>						
DRAG OBJECT	2	i.l.	0.257	0.845	t = 4.709 <b>P = 0.0005</b>	0.282
PUT OBJECT ON HEAD/BACK	5	i.l.	0.302	0.591	t = 2.662 <b>P = 0.024</b>	0.398
SHAKE OBJECT	19	<b>0.0001</b>	0.314	0.340	t = 7.684 <b>P &lt; 0.0001</b>	0.352
THROW OBJECT	6	0.125	0.411	0.056	t = 2.687 <b>P = 0.021</b>	0.598
HIT WITH OBJECT	5	i.l.	0.466	0.745	t = 4.962 <b>P = 0.0004</b>	0.491
<i>Non-communication tool-use actions</i>						
	9	0.267	0.224	0.221	t = 1.589 <b>P = 0.130</b>	0.540

Conspicuous-directed gestures are listed by sensory modality and for each sensory modality in relation to increasing Mean HI values. Characteristics, descriptive statistics and analyses for each conspicuous-directed gesture were taken from a previous publication (Prieur et al., 2016). N total: number of individuals who performed at least once the given manual activity; Data points total: total number of data points; N analysed: number of subjects who performed at least six times each the given manual activity; Data points analyzed: number of data points associated with the N analysed subjects; B test Lat. vs. Non-lat.: p-value of the binomial test on the number of lateralized versus non-lateralized individuals; LH: number of left-handed individuals; RH: number of right-handed individuals; B test LH vs. RH: p-value of the binomial test on the number of left-handed versus right-handed individuals; i.l.: number of lateralized subjects was insufficient for testing; Mean HI: Mean Handedness Index score of N analysed individuals, the sign indicates the direction of the manual bias (negative: left-hand bias, positive: right-hand bias); t-test: t-value and p-value of the t-test only for normally distributed HI values of N analysed individuals; Mean ABSHI: Mean Absolute value of Handedness Index score of N analysed individuals. Significant results are in bold.

**Table A3**  
Effect of the number of data points per individual on laterality for each manual activity.

Manual activity	Spearman correlation test between number of data points and HI values			Spearman correlation test between number of data points and ABSHI values		
<i>Conspicuous-directed gesture</i>						
DRAG OBJECT	rs = 0.017	P = 0.955	N = 13	rs = -0.097	P = 0.753	N = 13
PUT OBJECT ON HEAD/BACK	rs = 0.178	P = 0.601	N = 11	rs = -0.141	P = 0.680	N = 11
SHAKE OBJECT	rs = -0.163	P = 0.327	N = 38	rs = -0.277	P = 0.092	N = 38
THROW OBJECT	rs = -0.231	P = 0.470	N = 12	rs = -0.368	P = 0.239	N = 12
HIT WITH OBJECT	rs = -0.474	P = 0.119	N = 12	rs = -0.256	P = 0.422	N = 12
<i>Non-communication tool-use actions</i>						
	rs = 0.3358	P = 0.160	N = 19	rs = 0.1987	P = 0.4149	N = 19

Conspicuous-directed gestures are presented by sensory modality (four visual gestures then one tactile gesture) and for each sensory modality listed by alphabetic order; HI: Handedness Index; ABSHI: Mean Absolute value of Handedness Index; rs: Spearman's rho; P: Spearman's p-value; N: number of individuals who performed at least six times each the given manual activity.

**Table A4**  
Analysis of deviance (Type II Wald chi-square tests) for the best GLMM model.

Fixed terms and associated interactions	$\chi^2$	Df	P
Tool-use activity	8.031	1	0.005
Initiator's zoo	1.712	2	0.425
Initiator's age class	21.700	4	0.0002
Initiator's sex	0.895	1	0.344
Initiator's hierarchical rank	1.128	2	0.569
Tool-use activity × Initiator's zoo	6.931	2	<b>0.031</b>
Tool-use activity × Initiator's age class	46.003	4	<b>2.459e-09</b>
Tool-use activity × Initiator's sex	4.268	1	<b>0.039</b>
Tool-use activity × Initiator's hierarchical rank	43.253	2	<b>4.054e-10</b>

$\chi^2$ : type II Wald chi-square; Df: Degree of freedom; P: p-value of type II Wald chi-square. Significant results are in bold.

**Table A5**  
Results of post-hoc multiple comparisons for the best GLMM model: interaction between “Tool-use activity” and “Initiators’ zoo”.

Tool-use activity × Initiators’ zoo						
contrast			estimate	SE	z,ratio	P
C Tool use,Beauval	–	C Tool use,Leipzig	–0.243	0.212	–1.150	0.861
C Tool use,Beauval	–	C Tool use,Palmyre	0.030	0.217	0.137	1.000
C Tool use,Beauval	–	NC Tool use,Beauval	–1.734	0.628	–2.759	0.064
C Tool use,Leipzig	–	C Tool use,Palmyre	0.273	0.202	1.349	0.758
C Tool use,Leipzig	–	NC Tool use,Leipzig	–0.086	0.141	–0.610	0.990
C Tool use,Palmyre	–	NC Tool use,Palmyre	–1.786	0.715	–2.496	0.125
NC Tool use,Beauval	–	NC Tool use,Leipzig	1.404	0.668	2.104	0.285
NC Tool use,Beauval	–	NC Tool use,Palmyre	–0.022	0.523	–0.042	1.000
NC Tool use,Leipzig	–	NC Tool use,Palmyre	–1.426	0.740	–1.927	0.385

C Tool use: Communication tool use; NC Tool use: Non-communication tool use; contrast: difference between LSmeans; estimate: result of the difference between LSmeans; SE: Standard Error of the difference; z.ratio: ratio of the estimate to its standard error; P: Tukey’s p-value.

**Table A6**  
Results of post-hoc multiple comparisons for the best GLMM model: interaction between “Tool-use activity” and “Initiators’ age class”.

Tool-use activity × Initiators’ age class						
contrast			estimate	SE	z,ratio	P
C Tool use,Eld.	–	C Tool use,M.adu.	–1.190	0.293	–4.069	<b>0.002</b>
C Tool use,Eld.	–	C Tool use,Y.adu.	–1.073	0.306	–3.504	<b>0.017</b>
C Tool use,Eld.	–	C Tool use,Ado.	–0.841	0.256	–3.284	<b>0.035</b>
C Tool use,Eld.	–	C Tool use,Imm.	–0.824	0.298	–2.767	0.148
C Tool use,Eld.	–	NC Tool use,Eld.	0.284	0.609	0.465	1.000
C Tool use,Ado.	–	C Tool use,M.adu.	–0.349	0.283	–1.233	0.967
C Tool use,Ado.	–	C Tool use,Y.adu.	–0.231	0.251	–0.922	0.996
C Tool use,Ado.	–	NC Tool use,Ado.	–3.040	0.596	–5.104	<b>&lt; 0.0001</b>
C Tool use,Ado.	–	C Tool use,Imm.	0.017	0.316	0.054	1.000
C Tool use,Imm.	–	C Tool use,M.adu.	–0.366	0.343	–1.066	0.988
C Tool use,Imm.	–	C Tool use,Y.adu.	–0.248	0.347	–0.717	0.999
C Tool use,Imm.	–	NC Tool use,Imm.	3.839	0.521	7.372	<b>&lt; 0.0001</b>
C Tool use,M.adu.	–	C Tool use,Y.adu.	0.118	0.306	0.384	1.000
C Tool use,M.adu.	–	NC Tool use,M.adu.	–4.008	0.898	–4.466	<b>0.0003</b>
C Tool use,Y.adu.	–	NC Tool use,Y.adu.	–3.085	0.613	–5.032	<b>&lt; 0.0001</b>
NC Tool use,Eld.	–	NC Tool use,M.adu.	–5.482	0.853	–6.428	<b>&lt; 0.0001</b>
NC Tool use,Eld.	–	NC Tool use,Y.adu.	–4.441	0.699	–6.357	<b>&lt; 0.0001</b>
NC Tool use,Eld.	–	NC Tool use,Ado.	–4.165	0.673	–6.189	<b>&lt; 0.0001</b>
NC Tool use,Eld.	–	NC Tool use,Imm.	2.731	0.721	3.786	<b>0.006</b>
NC Tool use,Ado.	–	NC Tool use,M.adu.	–1.317	0.504	–2.616	0.210
NC Tool use,Ado.	–	NC Tool use,Y.adu.	–0.276	0.277	–0.999	0.992
NC Tool use,Ado.	–	NC Tool use,Imm.	6.896	1.035	6.665	<b>&lt; 0.0001</b>
NC Tool use,Imm.	–	NC Tool use,M.adu.	–8.213	1.271	–6.462	<b>&lt; 0.0001</b>
NC Tool use,Imm.	–	NC Tool use,Y.adu.	–7.172	1.058	–6.779	<b>&lt; 0.0001</b>
NC Tool use,M.adu.	–	NC Tool use,Y.adu.	1.041	0.503	2.070	0.549

C Tool use: Communication tool use; NC Tool use: Non-communication tool use; Imm.: Immature; Ado.: Adolescent; Y.adu.: Young adult; M.adu.: Mature adult; Eld.: Elder; contrast: difference between LSmeans; estimate: result of the 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.

**Table A7**

Results of post-hoc multiple comparisons for the best GLMM model: interaction between “Tool-use activity” and “Initiators’ sex”.

Tool-use activity × Initiators’ sex						
contrast			estimate	SE	z,ratio	P
C Tool use,F	–	C Tool use,M	0.257	0.211	1.215	0.617
C Tool use,F	–	NC Tool use,F	–0.611	0.255	–2.393	0.079
C Tool use,M	–	NC Tool use,M	–1.793	0.674	–2.661	<b>0.039</b>
NC Tool use,F	–	NC Tool use,M	–0.924	0.582	–1.587	0.386

C Tool use: Communication tool use; NC Tool use: Non-communication tool use; F: Female; M: Male; contrast: difference between LSmeans; estimate: result of the 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.

**Table A8**

Results of post-hoc multiple comparisons for the best GLMM model: interaction between “Tool-use activity” and “Initiators’ hierarchical rank”.

Tool-use activity × Initiators’ hierarchical rank						
contrast			estimate	SE	z,ratio	P
C Tool use,Dominant	–	C Tool use,Intermediate.	0.037	0.249	0.149	1.000
C Tool use,Dominant	–	C Tool use,Subordinate.	–0.021	0.311	–0.066	1.000
C Tool use,Dominant	–	NC Tool use,Dominant	1.867	0.355	5.261	< <b>0.0001</b>
C Tool use,Intermediate.	–	NC Tool use,Intermediate.	–0.909	0.568	–1.599	0.599
C Tool use,Intermediate.	–	C Tool use,Subordinate.	–0.058	0.244	–0.236	1.000
C Tool use,Subordinate.	–	NC Tool use,Subordinate.	–4.564	0.816	–5.593	< <b>0.0001</b>
NC Tool use,Dominant	–	NC Tool use,Intermediate.	–2.739	0.565	–4.851	< <b>0.0001</b>
NC Tool use,Dominant	–	NC Tool use,Subordinate.	–6.451	0.982	–6.568	< <b>0.0001</b>
NC Tool use,Intermediate.	–	NC Tool use,Subordinate.	–3.712	0.705	–5.265	< <b>0.0001</b>

C Tool use: Communication tool use; NC Tool use: Non-communication tool use; contrast: difference between LSmeans; estimate: result of the 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.

**Table A9**

Adjusted probabilities and confidence intervals associated with each interaction of the best GLMM model.

Tool-use activity × Zoo						
			Adjusted prob.	SE	asympt.LCL	asympt.UCL
C Tool use	–	Beauval	0.618	0.036	0.545	0.687
NC Tool use	–	Beauval	0.902	0.057	0.723	0.970
C Tool use	–	Leipzig	0.674	0.026	0.621	0.723
NC Tool use	–	Leipzig	0.693	0.032	0.628	0.751
C Tool use	–	Palmyre	0.611	0.041	0.530	0.687
NC Tool use	–	Palmyre	0.904	0.063	0.695	0.975

Tool-use activity × Initiators’ age class						
			Adjusted prob.	SE	asympt.LCL	asympt.UCL
C Tool use	–	Eld.	0.442	0.052	0.343	0.546
NC Tool use	–	Eld.	0.374	0.142	0.154	0.662
C Tool use	–	M.adu.	0.723	0.046	0.624	0.804
NC Tool use	–	M.adu.	0.993	0.006	0.962	0.999
C Tool use	–	Y.adu.	0.699	0.046	0.602	0.781
NC Tool use	–	Y.adu.	0.981	0.012	0.936	0.994
C Tool use	–	Ado.	0.648	0.043	0.561	0.726
NC Tool use	–	Ado.	0.975	0.015	0.921	0.992
C Tool use	–	Imm.	0.644	0.045	0.553	0.726
NC Tool use	–	Imm.	0.037	0.019	0.013	0.100

Tool-use activity × Initiators’ sex						
			Adjusted prob.	SE	asympt.LCL	asympt.UCL
C Tool use	–	F	0.664	0.024	0.615	0.710

(continued on next page)



Table A9 (continued)

Tool-use activity × Initiators' sex			Adjusted prob.	SE	asympt.LCL	asympt.UCL
NC Tool use	–	F	0.785	0.045	0.684	0.860
C Tool use	–	M	0.605	0.038	0.528	0.677
NC Tool use	–	M	0.902	0.060	0.711	0.972

Tool-use activity × Initiators' hierarchical rank			Adjusted prob.	SE	asympt.LCL	asympt.UCL
C Tool use	–	Dominant	0.636	0.035	0.565	0.703
NC Tool use	–	Dominant	0.213	0.062	0.116	0.359
C Tool use	–	Intermediate	0.628	0.040	0.547	0.702
NC Tool use	–	Intermediate	0.807	0.088	0.579	0.927
C Tool use	–	Subordinate	0.641	0.048	0.543	0.729
NC Tool use	–	Subordinate	0.994	0.005	0.972	0.999

C Tool use: Communication tool use; NC Tool use: Non-communication tool use; Imm.: Immature; Ado.: Adolescent; Y.adu.: Young adult; M.adu.: Mature adult; Eld.: Elder; F: Female; M: Male; Adjusted prob.: Adjusted probability; SE: Standard Error of the adjusted probability; asympt.LCL: asymptote for the Lower Confidence Limit; asympt.UCL: asymptote for the Upper Confidence Limit.

References

Ghirlanda, S., Vallortigara, G., 2004. The evolution of brain lateralization: a game-theoretical analysis of population structure. *Proc. R. Soc. Lond.* 271 (1541), 853–857. <http://dx.doi.org/10.1098/rspb.2003.2669>.

Ghirlanda, S., Frasnelli, E., Vallortigara, G., 2009. Intraspecific competition and coordination in the evolution of lateralization. *Philos. Trans. R. Soc. B: Biol. Sci.* 364 (1519), 861–866.

Schaafsma, S.M., Riedstra, B.J., Pfannkuche, K.A., Bouma, A., Groothuis, T.G.G., 2009. Epigenesis of behavioural lateralization in humans and other animals. *Philos. Trans. R. Soc. B: Biol. Sci.* 364 (1519), 915–927. [http://dx.doi.org/10.1016/S0003-3472\(71\)80002-7](http://dx.doi.org/10.1016/S0003-3472(71)80002-7).

Alonso, J.M., Castellano, A., Rodriguez, M., 1991. Behavioral lateralization in rats, prenatal stress effects on sex differences. *Brain Res.* 539, 4540. [http://dx.doi.org/10.1016/0006-8993\(91\)90684-n](http://dx.doi.org/10.1016/0006-8993(91)90684-n).

Altman, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–267. <http://dx.doi.org/10.1163/156853974X00534>.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear Mixed-Effects Models Using Eigen and S4. R Package Version 1.1-7. URL: <http://CRAN.R-project.org/package=lme4>.

Beck, B.B., 1980. *Animal Tool Behavior*. Garland STPM Pub.

Ben-Shachar, D., Zuk, R., Glinka, Y., 1995. Dopamine neurotoxicity: inhibition of mitochondrial respiration. *J. Neurochem.* 64 (2), 718–723.

Bertolucci-D'Angio, M., Serrano, A., Driscoll, P., Scatton, B., 1991. Involvement of mesocorticolimbic dopaminergic systems in emotional states. *Progress in Brain Research* Vol. 85. Elsevier, pp. 405–417.

Boesch, C., 1991. Handedness in wild chimpanzees. *Int. J. Primatol.* 12 (6), 541–558. <http://dx.doi.org/10.1007/BF02547669>.

Boesch, C., Boesch, H., 1990. Tool use and tool making in wild chimpanzees. *Folia Primatol.* 54 (1-2), 86–99. <http://dx.doi.org/10.1007/BF02373433>.

Bogart, S.L., Pruett, J.D., Ormiston, L.K., Russell, J.L., Meguerditchian, A., Hopkins, W.D., 2012. Termite fishing laterality in the fongoli savanna chimpanzees (*Pan troglodytes verus*): further evidence of a left hand preference. *Am. J. Phys. Anthropol.* 149, 591–598. <http://dx.doi.org/10.1002/ajpa.22175>.

Bourne, V.J., 2008. Examining the relationship between degree of handedness and degree of cerebral lateralization for processing facial emotion. *Neuropsychology* 22 (3), 350.

Breuer, T., Ndooundou-Hockemba, M., Fishlock, V., 2005. First observation of tool use in wild gorillas. *PLoS Biol.* 3 (11), e380.

Byrne, R.W., Corp, N., 2003. Acquisition of skilled gathering techniques in mahale chimpanzees. *Pan Afr. News* 10 (1), 4–7.

Cabeza, R., 2002. Hemispheric asymmetry reduction in older adults: the HAROLD model. *Psychol. Aging* 17 (1), 85.

Cabeza, R., Grady, C.L., Nyberg, L., McIntosh, A.R., Tulving, E., Kapur, S., Craik, F.I., et al., 1997. Age-related differences in neural activity during memory encoding and retrieval: a positron emission tomography study. *J. Neurosci.* 17 (1), 391–400.

Cantalupo, C., Hopkins, W.D., 2001. Asymmetric Broca's area in great apes. *Nature* 414–505. <http://dx.doi.org/10.1038/35107134>.

Cashmore, L., Uomini, N., Chapelain, A., 2008. The evolution of handedness in humans and great apes, a review and current issues. *J. Anthropol. Sci. = Rivista Di Antropologia, JASS/Istituto Italiano Di Antropologia* 86, 7–35.

Chapelain, A.S., Hogervorst, E., 2009. Hand preferences for bimanual coordination in 29 bonobos (*Pan paniscus*). *Behav. Brain Res.* 196 (1), 15–29. <http://dx.doi.org/10.1016/j.bbr.2008.07.012>.

Corballis, M.C., 2002. *From Hand to Mouth: The Origins of Language*. Princeton University Press.

Creel, S., 2001. Social dominance and stress hormones. *Trends Ecol. Evol.* 16 (9), 491–497. [http://dx.doi.org/10.1016/S0169-5347\(01\)02227-3](http://dx.doi.org/10.1016/S0169-5347(01)02227-3).

Creel, S., Creel, N.M., Monfort, S.L., 1996. Social stress and dominance. *Nature* 379, 212. <http://dx.doi.org/10.1038/379212a0>.

De Bellis, M.D., 2005. The psychobiology of neglect. *Child Maltreat.* 10 (2), 150–172. <http://dx.doi.org/10.1177/1077559505275116>.

de Vries, H., 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Anim. Behav.* 50, 1375–1389. [http://dx.doi.org/10.1016/0003-3472\(95\)80053-0](http://dx.doi.org/10.1016/0003-3472(95)80053-0).

de Vries, H., Stevens, J.M.G., Vervaecke, H., 2006. Measuring and testing the steepness of dominance hierarchies. *Anim. Behav.* 71, 585–592. <http://dx.doi.org/10.1016/j.anbehav.2005.05.015>.

Deckel, A.W., 1998. Hemispheric control of territorial aggression in *Anolis carolinensis*: effects of mild stress. *Brain Behav. Evol.* 51, 33–39. <http://dx.doi.org/10.1159/00006527>.

Drea, C.M., Wallen, K., Akinbami, M.A., Mann, D.R., 1995. Neonatal testosterone and handedness in yearling rhesus monkeys (*Macaca mulatta*). *Physiol. Behav.* 58, 1257–1262. [http://dx.doi.org/10.1016/0031-9384\(95\)02026-8](http://dx.doi.org/10.1016/0031-9384(95)02026-8).

Forrester, G.S., Leavens, D.A., Quaresmini, C., Vallortigara, G., 2011. Target animacy influences gorilla handedness. *Anim. Cogn.* 14 (6), 903–907.

Forrester, G.S., Quaresmini, C., Leavens, D.A., Spiezio, C., Vallortigara, G., 2012. Target animacy influences chimpanzee handedness. *Anim. Cogn.* 15 (6), 1121–1127.

Forrester, G.S., Quaresmini, C., Leavens, D.A., Mareschal, D., Thomas, M.S., 2013. Human handedness: an inherited evolutionary trait. *Behav. Brain Res.* 237, 200–206. <http://dx.doi.org/10.1016/j.bbr.2012.09.037>.

Foucart, J., Bril, B., Hirata, S., Morimura, N., Houki, C., Ueno, Y., Matsuzawa, T., 2005. A Preliminary Analysis of Nut-Cracking Movements in a Captive Chimpanzee: Adaptation to the Properties of Tools and Nuts. *Stone Knapping, the Necessary Conditions for a Uniquely Hominid Behaviour*. McDonald Institute Monograph Series, Cambridge, pp. 147–158.

Fox, J., Weisberg, S., 2011. *An R Companion to Applied Regression*, Second edition. Sage, Thousand Oaks. <http://dx.doi.org/10.1080/10543406.2012.635980>.

Gannon, P.J., Holloway, R.L., Broadfield, D.C., Braun, A.R., 1998. Asymmetry of chimpanzee planum temporale: humanlike pattern of Wernicke's brain language area homolog. *Science* 279 (5348), 220–222.

Goodall, J., 1986. *The Chimpanzees of Gombe: Patterns in Adaptation*. Harvard University Press, Cambridge.

Grady, C.L., Randy McIntosh, A., Horwitz, B., Rapoport, S.I., 2000. Age-related changes in the neural correlates of degraded and nondegraded face processing. *Cognit. Neuropsychol.* 17 (1–3), 165–186.

Greenfield, P.M., 1991. From hand to mouth. *Behav. Brain Sci.* 14 (04), 577–595. <http://dx.doi.org/10.1017/S0140525X0007148X>.

Grueter, C.C., Robbins, M.M., Ndagijimana, F., Stoinski, T.S., 2013. Possible tool use in a mountain gorilla. *Behav. Processes* 100, 160–162.

Hare, B., 2001. Can competitive paradigms increase the validity of experiments on primate social cognition? *Anim. Cogn.* 4 (3-4), 269–280. <http://dx.doi.org/10.1007/s100710100084>.

Harris, L.J., Carlson, D.F., 1993. *Hand preference for visually-guided reaching in human infants and adults. Primate Laterality*. Springer, New York, pp. 285–305. <http://dx.doi.org/10.1017/S0140525X00054339>.

Hervé, M., 2014. RVAideMemoire: Diverse Basic Statistical and Graphical Functions. URL: R Package Version 0.9-40. <http://CRAN.R-project.org/package=RVAideMemoire>.

Higuchi, S., Chaminade, T., Imamizu, H., Kawato, M., 2009. Shared neural correlates for language and tool use in Broca's area. *Neuroreport* 20 (15), 1376–1381. <http://dx.doi.org/10.1097/WNR.0b013e3283315570>.

- Hobaiter, C., Byrne, R.W., 2013. Laterality in the gestural communication of wild chimpanzees. *Ann. N. Y. Acad. Sci.* 1288 (1), 9–16. <http://dx.doi.org/10.1111/nyas.12041>.
- Hohmann, G., Fruth, B., 2003. Culture in bonobos? Between-species and with-species variation in behavior. *Curr. Anthropol.* 44, 563–571. <http://dx.doi.org/10.1086/377649>.
- Hopkins, W.D., 1993. Posture and reaching in chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*). *J. Comp. Psychol.* 107 (2), 162–168. <http://dx.doi.org/10.1037/0735-7036.107.2.162>.
- Hopkins, W.D., 2006. Comparative and familial analysis of handedness in great apes. *Psychol. Bull.* 132 (4), 538.
- Hopkins, W.D., Cantalupo, C., 2004. Handedness in chimpanzees (*Pan troglodytes*) is associated with asymmetries of the primary motor cortex but not with homologous language areas. *Behav. Neurosci.* 118 (6), 1176–1183. <http://dx.doi.org/10.1037/0735-7044.118.6.1176>.
- Hopkins, W.D., de Waal, F.B.M., 1995. Behavioral laterality in captive bonobos (*Pan paniscus*): replication and extension. *Int. J. Primatol.* 16, 261–276. <http://dx.doi.org/10.1007/BF02735481>.
- Hopkins, W.D., Leavens, D.A., 1998. Hand use and gestural communication in chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 112 (1), 95–99. <http://dx.doi.org/10.1037/0735-7036.112.1.95>.
- Hopkins, W.D., Nir, T., 2010. Planum temporale surface area and grey matter asymmetries in chimpanzees (*Pan troglodytes*): the effect of handedness and comparison with findings in humans. *Behav. Brain Res.* 208 (2), 436–443.
- Hopkins, W.D., Bennett, A.J., Bales, S.L., Lee, J., Ward, J.P., 1993. Behavioral laterality in captive bonobos (*Pan paniscus*). *J. Comp. Psychol.* 107 (4), 403–410. <http://dx.doi.org/10.1037/0735-7036.107.4.403>.
- Hopkins, W.D., Wesley, M.J., Kay Izard, M., Hook, M., Schapiro, S.J., 2004. Chimpanzees (*Pan troglodytes*) are predominantly right-handed: replication in three populations of apes. *Behav. Neurosci.* 118 (3), 659–663. <http://dx.doi.org/10.1037/0735-7044.118.3.659>.
- Hopkins, W.D., Russell, J.L., Cantalupo, C., Freeman, H., Schapiro, S.J., 2005a. Factors influencing the prevalence and handedness for throwing in captive chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 119 (4), 363–370. <http://dx.doi.org/10.1037/0735-7036.119.4.363>.
- Hopkins, W.D., Russell, J.L., Freeman, H., Buehler, N., Reynolds, E., Schapiro, S.J., 2005b. The distribution and development of handedness for manual gestures in captive chimpanzees (*Pan troglodytes*). *Psychol. Sci.* 6, 487–493. <http://dx.doi.org/10.1111/j.0956-7976.2005.01561.x>.
- Hopkins, W.D., Russell, J.L., Cantalupo, C., 2007. Neuroanatomical correlates of handedness for tool use in chimpanzees (*Pan troglodytes*) implication for theories on the evolution of language. *Psychol. Sci.* 18 (11), 971–977.
- Hopkins, W.D., Russell, J.L., Schaeffer, J.A., Gardner, M., Schapiro, S.J., 2009. Handedness for tool use in captive chimpanzees (*Pan troglodytes*): sex differences, performance, heritability and comparison to the wild. *Behaviour* 146 (11), 1463–1483. <http://dx.doi.org/10.1163/156853909X441005>.
- Hopkins, W.D., Pika, S., Liebal, K., Bania, A., Meguerditchian, A., Gardner, M., Schapiro, S., 2012. Handedness for manual gestures in great apes: a meta-analysis. In: Pika, S., Liebal, K. (Eds.), *Developments in Primate Gesture Research*. John Benjamin's Publishing Company, Amsterdam, pp. 93–110. <http://dx.doi.org/10.17617/2.2248195>.
- Hughes, S., Gibbs, J., Dunlop, D., Edelman, P., Singer, R., et al., 1997. Predictors of decline in manual performance in older adults. *J. Am. Geriatr. Soc.* 45, 905–910. <http://dx.doi.org/10.1111/j.1532-5415>.
- Joseph, R., 1994. The limbic system and the foundations of emotional experience. *Encycl. Hum. Behav.* 67–81.
- Josse, G., Tzourio-Mazoyer, N., 2004. Hemispheric specialization for language. *Brain Res. Rev.* 44 (1), 1–12.
- Kalisch, T., Wilimzig, C., Kleibel, N., Tegenthoff, M., Dinse, H.R., 2006. Age-related attenuation of dominant hand superiority. *PLoS One* 1 (1), e90. <http://dx.doi.org/10.1371/journal.pone.0000090>.
- Kano, T., 1982. The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. *Primates* 23, 17188. <http://dx.doi.org/10.1007/BF02381159>.
- Kano, T., 1998. A preliminary glossary of bonobo behaviors at Wamba. In: Nishida, T. (Ed.), *Comparative Study of the Behavior of the Genus Pan* by Compiling Video Ethogram. Nissho Printer, Kyoto, pp. 39–81.
- Kimura, D., 1973. Manual activity during speaking—I. Right-handers. *Neuropsychologia* 11 (1), 45–50. [http://dx.doi.org/10.1016/0028-3932\(73\)90063-8](http://dx.doi.org/10.1016/0028-3932(73)90063-8).
- 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. <http://dx.doi.org/10.1093/brain/123.12.2512>.
- Lacreuse, A., Fragaszy, D., 1999. Left hand preferences in capuchins (*Cebus apella*), role of spatial demands in manual activity. *Laterality* 4 (1), 65. <http://dx.doi.org/10.1080/713754321>.
- Langbein, J., Puppe, B., 2004. Analysing dominance relationships by sociometric methods—a plea for a more standardised and precise approach in farm animals. *Appl. Anim. Behav. Sci.* 87, 293–315. <http://dx.doi.org/10.1016/j.applanim.2004.01.007>.
- Lenth, R.V., 2014. Lsmmeans: Least-Squares Means. URL: R Package Version 2.11. <http://CRAN.R-project.org/package=lsmmeans>.
- Lonsdorf, E.V., Hopkins, W.D., 2005. Wild chimpanzees show population level handedness for tool use. *Proc. Natl. Acad. Sci. U. S. A.* 102, 12634–12638. <http://dx.doi.org/10.1073/pnas.0505806102>.
- Lorincz, E., Fabre-Thorpe, M., 1996. Shift of laterality and compared analysis of paw performance in cats during practice of a visuomotor task. *J. Comp. Psychol.* 110 (3), 307–315. <http://dx.doi.org/10.1037/0735-7036.110.3.307>.
- Maille, A., Chapelain, A., Deruti, L., Bec, P., Blois-Heulin, C., 2013. Manual laterality for pointing gestures compared to grasping actions in guenons and mangabeys. *Anim. Behav.* 86 (4), 705–716. <http://dx.doi.org/10.1016/j.anbehav.2013.06.016>.
- Marchant, L.F., McGrew, W.C., 1991. Laterality of function in apes: a meta-analysis of methods. *J. Hum. Evol.* 21, 425–438. [http://dx.doi.org/10.1016/0047-2484\(91\)90093-B](http://dx.doi.org/10.1016/0047-2484(91)90093-B).
- Markham, A.C., Santymire, R.M., Lonsdorf, E.V., Heintz, M.R., Lipende, I., Murray, C.M., 2014. Rank effects on social stress in lactating chimpanzees. *Anim. Behav.* 87, 195–202. <http://dx.doi.org/10.1016/j.anbehav.2013.10.031>.
- Martin, P., Bateson, P., 1994. *Measuring Behaviour: an Introductory Guide*, 2nd ed. Cambridge University Press <http://dx.doi.org/10.1017/CBO9781139168342>.
- McGrew, W.C., Marchant, L.F., 1992. Chimpanzees, tools, and termites, hand preference or handedness? *Curr. Anthropol.* 33 (1), 114–119. <http://dx.doi.org/10.1086/204041>.
- 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. *Yearb. Phys. Anthropol.* 40, 201–232. [http://dx.doi.org/10.1002/\(SICI\)1096-8644\(1997\)25+ <201::AID-AJPA8>3.0.CO;2-6](http://dx.doi.org/10.1002/(SICI)1096-8644(1997)25+ <201::AID-AJPA8>3.0.CO;2-6).
- McManus, I.C., 1991. *The inheritance of left-handedness*. *Biological Asymmetry and Handedness* (Ciba Foundation Symposium), vol. 162. Wiley, Chichester, pp. 251–281.
- Meguerditchian, A., Vauclair, J., 2006. Baboons communicate with their right hand. *Behav. Brain Res.* 171 (1), 170–174. <http://dx.doi.org/10.1016/j.bbr.2006.03.018>.
- 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 Lang.* 108 (3), 167–174. <http://dx.doi.org/10.1016/j.bandl.2008.10.004>.
- Meguerditchian, A., Vauclair, J., Hopkins, W.D., 2010a. 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. <http://dx.doi.org/10.1016/j.cortex.2009.02.013>.
- Meguerditchian, A., Calcutt, S.E., Lonsdorf, E.V., Ross, S.R., Hopkins, W.D., 2010b. Captive gorillas are right-handed for bimanual feeding. *Am. J. Phys. Anthropol.* 141 (4), 638–645. <http://dx.doi.org/10.1002/ajpa.21244>.
- Meguerditchian, A., Molesti, S., Vauclair, J., 2011. Right-handedness predominance in 162 baboons (*Papio anubis*) for gestural communication: consistency across time and groups. *Behav. Neurosci.* 125 (4), 653–660. <http://dx.doi.org/10.1037/a0023823>.
- Meguerditchian, A., Gardner, M.J., Schapiro, S.J., Hopkins, W.D., 2012. The sound of one hand clapping: handedness and perisylvian neural correlates of a communicative gesture in chimpanzees. *Proc. R. Soc. Biol.* 279, 1959–1966. <http://dx.doi.org/10.1098/rspb.2011.2485>.
- 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. *Dev. Psychobiol.* 55, 637–650. <http://dx.doi.org/10.1002/dev.21150>.
- Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., Boesch, C., 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proc. Natl. Acad. Sci.* 104 (9), 3043–3048.
- Meunier, H., Vauclair, J., Fagard, J., 2012. Human infants and baboons show the same pattern of handedness for a communicative gesture. *PLoS One* 7 (3), e33959. <http://dx.doi.org/10.1371/journal.pone.0033959>.
- Meunier, H., Fizez, J., Vauclair, J., 2013. Tonkean macaques communicate with their right hand. *Brain Lang.* 126 (2), 181–187.
- Muller, M.N., Wrangham, R.W., 2004. Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* 55 (4), 332–340. <http://dx.doi.org/10.1007/s00265-003-0713-1>.
- Nielson, K.A., Langenecker, S.A., Garavan, H., 2002. Differences in the functional neuroanatomy of inhibitory control across the adult life span. *Psychol. Aging* 17 (1), 56.
- Nishida, T., Zamma, K., Matsusaka, T., Inaba, A., McGrew, W.C. (Eds.), 2010. *Chimpanzee Behavior in the Wild: An Audio-Visual Encyclopedia*. Springer, Tokyo. [http://dx.doi.org/10.1007/978-4-431-53895-0\\_3](http://dx.doi.org/10.1007/978-4-431-53895-0_3).
- Ocklenburg, S., Korte, S.M., Peterburs, J., Wolf, O.T., Güntürkün, O., 2016. Stress and laterality—the comparative perspective. *Physiol. Behav.* 164, 321–329.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9 (1), 97–113.
- Palmer, A.R., 2002. Chimpanzee right-handedness reconsidered: evaluating the evidence with funnel plots. *Am. J. Phys. Anthropol.* 118 (2), 191–199. <http://dx.doi.org/10.1002/ajpa.10063>.
- Paquette, D., 1992. Discovering and learning tool-use for fishing honey by captive chimpanzees. *Hum. Evol.* 7 (3), 17–30.
- Pika, S., 2008a. Gestures of apes and pre-linguistic human children: similar or different? *First Lang.* 28 (2), 116–140. <http://dx.doi.org/10.1177/0142723707080966>.
- Pika, S., 2008b. What is the nature of the gestural communication of great apes? In: Zlatev, J., Racine, T., Sinha, C., Itkonen, E. (Eds.), *The Shared Mind*. John Benjamins Publishing Company, Amsterdam, pp. 165–186. <http://dx.doi.org/10.1038/ncomms1567>.
- Pika, S., Bugnyar, T., 2011. The use of referential gestures in ravens (*Corvus corax*) in the wild. *Nat. Commun.* 2, 560. <http://dx.doi.org/10.1038/ncomms1567>.
- Pollick, A.S., de Waal, F., 2007. Ape gestures and language evolution. *Proc. Natl. Acad. Sci. U. S. A.* 104, 8184–8189. <http://dx.doi.org/10.1073/pnas.0702624104>.
- Prieur, J., 2015. *Chimpanzees' and Gorillas' Intraspecific Gestural Laterality: A Multifactorial Investigation*. Doctorate Thesis. URL: University of Rennes 1, France. [www.theses.fr/en/2015REN1S056](http://theses.fr/en/2015REN1S056).
- Prieur, J., Pika, S., Barbu, S., Blois-Heulin, C., 2016. A multifactorial investigation of captive chimpanzees' intraspecific gestural laterality. *Anim. Behav.* 116, 31–43. <http://dx.doi.org/10.1016/j.anbehav.2016.03.024>.
- Pujol, J., Deaus, J., Losilla, J.M., Capdevila, A., 1999. Cerebral lateralization of language

- in normal left-handed people studied by functional MRI. *Neurology* 52, 1038–1043.
- R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria URL: <http://www.R-project.org>.
- Ranganathan, V.K., Siemionow, V., Sahgal, V., Yue, G.H., 2001. Effects of aging on hand function. *J. Am. Geriatr. Soc.* 49 (11), 1478–1484. <http://dx.doi.org/10.1046/j.1532-5415.2001.4911240.x>.
- Reuter-Lorenz, P.A., Jonides, J., Smith, E.E., Hartley, A., Miller, A., Marshuetz, C., Koeppel, R.A., 2000. Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. *J. Cognit. Neurosci.* 12 (1), 174–187.
- Rogers, L.J., Vallortigara, G., Andrew, R.J., 2013. *Divided Brains: The Biology and Behaviour of Brain Asymmetries*. Cambridge University Press.
- Rohlf, P., Ramirez, J.M., 2006. Aggression and brain asymmetries: a theoretical overview. *Aggress. Violent Behav.* 11, 283–297. <http://dx.doi.org/10.1016/j.avb.2005.09.001>.
- Schore, A.N., 1997. Early organization of the nonlinear right brain and development of a predisposition to psychiatric disorders. *Dev. Psychopathol.* 9 (4), 595–631.
- Schut, L.J., 1998. Motor system changes in the aging brain: what is normal and what is not. *Geriatrics* 53 (1), S16–19.
- Schweitzer, C., Bec, P., Blois-Heulin, C., 2007. Does the complexity of the task influence manual laterality in De Brazza's monkeys (*Cercopithecus neglectus*)? *Ethology* 113 (10), 983–994. <http://dx.doi.org/10.1111/j.1439-0310.2007.01405.x>.
- Siegel, S., Castellan, N.J., 1988. *Nonparametric Statistics for the Behavioural Sciences*. McGraw-Hill, Singapore.
- Spinozzi, G., Cacchiarelli, B., 2000. Manual laterality in haptic and visual reaching tasks by tufted capuchin monkeys (*Cebus apella*). An association between hand preference and hand accuracy for food discrimination. *Neuropsychologia* 38 (13), 1685–1692. [http://dx.doi.org/10.1016/S0028-3932\(00\)00080-4](http://dx.doi.org/10.1016/S0028-3932(00)00080-4).
- Springer, J.A., Binder, J.R., Hammeke, T.A., Swanson, S.J., Frost, J.A., Bellgowan, P.S., et al., 1999. Language dominance in neurologically normal and epilepsy subjects: a functional MRI study. *Brain* 122 (11), 2033–2046.
- Stout, D., Chaminade, T., 2012. Stone tools, language and the brain in human evolution. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 367 (1585), 75–87.
- Vallortigara, G., Versace, E., 2017. Laterality at the neural, cognitive, and behavioral levels. In: Call, J., Burghardt, G.M., Pepperberg, I.M., Snowden, C.T., Zentall, T. (Eds.), *APA Handbooks in Psychology. APA Handbook of Comparative Psychology: Basic Concepts, Methods, Neural Substrate, and Behavior*, pp. 557–577.
- Van Lawick-Goodall, J., 1970. Tool-using in primates and other vertebrates. In: Lehrman, D., Hinde, R., Shaw, E. (Eds.), *Advances in the Study of Behavior*, vol. 3. Academic Press, New York, pp. 195–249.
- Van Schaik, C.P., Fragaszy, D., Perry, S., 2003. Local traditions in orangutans and chimpanzees: social learning and social tolerance. *Biol. Traditions Models Evid.* 297–328.
- Versace, E., Vallortigara, G., 2015. Forelimb preferences in human beings and other species: multiple models for testing hypotheses on lateralization. *Front. Psychol.* 6, 233.
- Waller, B.M., Warmelink, L., Liebal, K., Micheletta, J., Slocombe, K.E., 2013. Pseudoreplication: a widespread problem in primate communication research. *Anim. Behav.* 86 (2), 483–488. <http://dx.doi.org/10.1016/j.anbehav.2013.05.038>.
- Warren, J., 1980. Handedness and laterality in humans and other animals. *Physiol. Psychol.* 8, 351–359. <http://dx.doi.org/10.3758/BF03337470>.
- Weiss, D.J., Newport, E.L., 2006. Mechanisms underlying language acquisition: benefits from a comparative approach. *Infancy* 9 (2), 241–257.
- Westergaard, G.C., Lussier, I.D., 1999. Left-handedness and longevity in primates. *Int. J. Neurosci.* 99, 79–87. <http://dx.doi.org/10.3109/00207459908994315>.
- Westergaard, G.C., Suomi, S.J., 1993. Hand preference in capuchin monkeys varies with age. *Primates* 34 (3), 295–299. <http://dx.doi.org/10.1007/BF02382624>.
- Westergaard, G.C., Suomi, S.J., 1994. Asymmetrical manipulation in the use of tools by tufted capuchin monkeys (*Cebus apella*). *Folia Primatol.* 63, 96–98. <http://dx.doi.org/10.1159/000156799>.
- Westergaard, G.C., Lussier, I.D., Suomi, S.J., 2000. Hormonal correlates of hand preference in free-ranging primates. *Neuropsychopharmacology* 23, 502–507. [http://dx.doi.org/10.1016/S0893-133X\(00\)00141-X](http://dx.doi.org/10.1016/S0893-133X(00)00141-X).
- Westergaard, G.C., Chavanne, T.J., Lussier, I.D., Houser, L., Cleveland, A., 2003. Left-handedness is correlated with CSF monoamine metabolite and plasma cortisol concentrations, and with impaired sociality, in free-ranging adult male rhesus macaques (*Macaca mulatta*). *Laterality* 8, 169–187. <http://dx.doi.org/10.1080/713754484>.
- Whitehead, H., 2008. *Analyzing Animal Societies, Quantitative Methods for Vertebrate Social Analysis*. The University of Chicago Press, Chicago, IL. <http://dx.doi.org/10.1016/j.anbehav.2009.04.010>.
- Wilson, E.O., 1975. *Sociobiology, The New Synthesis*. Belknap Press of Harvard University Press, Cambridge, MA. <http://dx.doi.org/10.1023/A:1004845822189>.
- Wittig, R.M., Boesch, C., 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *Int. J. Primatol.* 24 (4), 847–867. <http://dx.doi.org/10.1023/A:1024632923180>.
- Xu, J., Gannon, P.J., Emmorey, K., Smith, J.F., Braun, A.R., 2009. Symbolic gestures and spoken language are processed by a common neural system. *Proc. Natl. Acad. Sci.* 106 (49), 20664–20669. <http://dx.doi.org/10.1073/pnas.0909197106>.