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Captive gorillas' manual laterality: The impact of gestures, manipulators and interaction specificity

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ABSTRACT

Relationships between humans' manual laterality in non-communicative and communicative functions are still poorly understood. Recently, studies showed that chimpanzees' manual laterality is influenced by functional, interactional and individual factors and their mutual intertwinement. However, what about manual laterality in species living in stable social groups? We tackled this question by studying three groups of captive gorillas (N = 35) and analysed their most frequent manual signals: three manipulators and 16 gesture types. Our multifactorial investigation showed that conspecific-directed gestures were overall more right-lateralized than conspecific-directed manipulators. Furthermore, it revealed a difference between conspecific- and human-directed gestural laterality for signallers living in one of the study groups. Our results support the hypothesis that gestural laterality is a relevant marker of language left-brain specialisation. We suggest that components of communication and of manipulation (not only of an object but also of a conspecific) do not share the same lateralised cerebral system in some primate species.

1. Introduction

Humans' left-hemisphere specialisation for both manipulative and communicative interactions is well documented (e.g. Hecaen & Ajuriaguerra, 1964; Kimura, 1973). However, the relationship between humans' manual laterality in non-communicative and communicative functions is relatively poorly understood (e.g. see Cochet & Byrne, 2013 for a review). To date, so far only Cochet and Vauclair (2012) and Cochet, Jover, Oger, and Vauclair (2014) investigated this aspect by carrying out an experimental study on human adults with a special focus on actions and a specific communicative gesture, POINTING.[1] For example, they reported that individuals used their right hands more frequently for bimanual coordinated manipulations[2] than for POINTING produced without speech. Moreover, the authors found no significant difference in the direction of laterality between bimanual coordinated manipulations and POINTING produced with speech. These findings indicate the ambiguous relationship between the direction of manual asymmetry for manipulations and language left-brain specialisation. Additional studies are, however, crucially needed. A considerable amount of research has focused on the phylogenetic origins and functions of hemispheric specialisation of human laterality by investigating related characteristics in our closest living relatives, the non-human primates (hereafter primates) (e.g. Hopkins, 2007; Hopkins et al., 2012; Vauclair, Fagot, & Dépy, 1999). Many primate species show a right-hand bias at the population-level for manipulation tasks requiring high levels of complexity such as for instance bimanual coordinated actions (e.g. bimanual coordinated tube task for chimpanzees, *Pan troglodytes*: Hopkins, 1995; bimanual feeding for western lowland gorillas, *Gorilla gorilla gorilla*: Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010). On the contrary, recent research showed that manipulation tasks requiring low levels of complexity, such as for example spontaneous uni-manual actions, do not reveal manual laterality at the population-level (e.g. unimanual food reaching for chimpanzees: Hopkins & Rabinowitz, 1997; western lowland gorillas: Meguerditchian, Calcutt, et al., 2010; De Brazza's monkeys, *Cercopithecus neglectus*: Schweitzer, Bec, & Blois-Heulin, 2007). Moreover, an increasing body of work indicates that right hands are used more frequently for gestural communication than for manipulations (e.g. see Meguerditchian, Vauclair, & Hopkins, 2013 for a review). These findings led researchers to postulate that laterality in primates' gestural communication represents a precursor of the left-hemispheric lateralisation for human language (e.g. see

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[1] From here on gestures are depicted in small capitals.

[2] Bimanual coordinated actions require the use of two hands for different but complementary roles (e.g. for bimanual coordinated manipulation of an object, one hand simply holds the object while the other hand is engaged in a more active/complex action).

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Meguerditchian & Vauclair, 2014 for a review). This hypothesis is based on a number of observational and experimental studies of primates' gestural communication (e.g. Arbib, Liebal, & Pika, 2008). For instance, (1) great apes' gestural signalling is more flexible than their vocal production (e.g. Call & Tomasello, 2007; see for different view Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013), (2) mirror neurons in the rhesus monkey's premotor cortex (area F5) discharge both when a subject performs a given action and when it observes the same action being performed by an experimenter (see Fabbri-Destro & Rizzolatti, 2008 for a review), and (3) many species of primates, particularly great apes such as chimpanzees and gorillas, present a right gestural laterality (e.g. Prieur, Pika, Barbu, & Blois-Heulin, 2016a, 2016b; see also Hopkins et al., 2012 for a review).

However, most studies investigating primates' gestural laterality have focused on distinct gestures types, such as human-directed gestures (e.g. Hopkins & Leavens, 1998) or gestures used towards both humans and conspecifics (pooled data) (e.g. Meguerditchian, Vauclair, & Hopkins, 2010). Interestingly, recent studies showed that social pressures can affect laterality (e.g. Chapelain et al., 2015; Prieur et al., 2016a; Schaafsma, Riedstra, Pfannkuche, Bouma, & Groothuis, 2009; Prieur, Pika, Barbu, & Blois-Heulin, 2017). For instance, Prieur, Lemasson, Barbu, & Blois-Heulin (submitted for publication-a) showed that social pressures, particularly from the study subjects (conspecifics) but also to a lesser extent from the experimenters, are likely to influence the results of experimental laterality studies. To understand in more detail the factors influencing laterality, it is thus crucial to investigate the spontaneous use of gestures in naturally occurring interactions with conspecifics. So far, only a relatively small number of studies have addressed gestural laterality in naturally occurring interactions between conspecifics although (i) socio-ecological validity is particularly relevant from an evolutionary point of view, and (ii) several researchers have suggested that intraspecific interactions could explain population-level laterality (Ghirlanda, Frasnelli, & Vallortigara, 2009). Furthermore, Prieur, Pika, Barbu, and Blois-Heulin (submitted for publication-b) recently showed that chimpanzees' gestural laterality varied in relation to various aspects such as specificity of recipient (conspecifics vs. humans), spatial position of recipient (in or outside signaller's visual field), and signallers' age. These findings emphasize the necessity to apply multifactorial investigations to study laterality of intentional signals in detail to avoid biases and ambiguous results.

According to Liebal and Call (2012), gestures (mechanically ineffective movements of limbs, head or body movements, which are directed to recipients and result in a voluntary response; Pika, 2008) would originate from actions (mechanically effective) deprived of a communicative function (but see for a different opinion: Pika & Fröhlich, submitted for publication; Prieur et al., submitted for publication-b). Therefore, their function and use can be described along a continuum (see, Scott & Pika, 2012), suggesting that their physical forms are the same, sometimes mechanically effective and sometimes mechanically ineffective, directed or non-directed and eliciting or not a voluntary response. In the evolutionary context of the origin of human right handedness and cerebral specialisation for language, the lively debate concerning the origins of gesture acquisition (see Byrne et al., 2017; Fröhlich, Wittig, & Pika, 2016; Liebal & Call, 2012; Pika & Fröhlich, submitted for publication) raises several issues ranging from the contribution of our ancestors' manual actions directed towards a social partner (from here noted "manipulators") over the emergence of the left-hemisphere language specialisation of modern humans, to the lateralised cerebral structures controlling manipulators and gestures performed in signalling contexts. To address these issues, it is important to investigate the influence of mechanical effectiveness and communication type on manual laterality of the closest phylogenetic species to humans, the great apes.

To date, we know relatively little about the extent of manual laterality with regards to (i) different social structures and dynamics (ii) different spontaneous activities directed towards conspecifics (manipulation actions versus gestures), and (iii) communication types (conspecific- versus human-directed gestures). However, investigations into these aspects are essential to understand relationships between human functional brain specialisation, speech, handedness for gestures and social life. Very recently, Prieur and colleagues (2017, submitted for publication-b) performed for the first time such investigations. First, they compared manual laterality between gorillas and chimpanzees focusing on intraspecific gestures (Prieur et al., 2017). Gorillas are as genetically distant from chimpanzees as they are from humans (Kaessmann, Wiebe, Weiss, & Pääbo, 2001). They show different social structures and dynamics: gorillas live in polygamous and generally stable and cohesive groups (e.g. Bradley, Doran-Sheehy, Lukas, Boesch, & Vigilant, 2004; Schaller, 1963; Watts, 1996) whereas chimpanzees have less stable social structures since they live in fission-fusion societies characterised by a highly variable party membership (e.g. Goodall, 1986; Mitani, 2009). Based on their findings, Prieur and colleagues hypothesized that differences between gestural laterality patterns of the two species may be the consequence of differences in social structure and dynamics.

Second, they investigated the influence of mechanical effectiveness and communication type on chimpanzees' manual laterality (Prieur et al., submitted for publication-b). They found that signallers' right-hand use was more pronounced for conspecific-directed gestures than for manipulations directed towards conspecifics. Furthermore, they showed that conspecific- and human-directed gestural lateralities were modulated differently by the recipient's position with regards to the signaller's visual field and age. However, how do mechanical effectiveness and of recipient specificity impact upon laterality inspecies living in stable social groups? To tackle this central question, the present study adopted a comparative approach and apply the same study design and multifactorial approach used previously (Prieur et al., submitted for publication-b). We assessed manual laterality of gorillas in three different, distinct categories of intentional signals: conspecific-directed manipulators, conspecific-directed gestures and human-directed gestures. Choosing gorillas as model system for the present study and comparing results between both great ape species will enable us to assess the influence of the social-related factors on intraspecific manual signal laterality. We addressed the following three questions:

(1) Do gorillas show a right-hand bias at the population-level for conspecific-directed manipulators (mechanically effective) and for human-directed gestures (mechanically ineffective), as we previously found for conspecific-directed gestures in chimpanzees and gorillas (Prieur et al., 2016a, 2016b)? To investigate this question, we studied the direction of manual laterality at the population level for each behavioural category separately.

Based on recent findings on primates' laterality in both spontaneous gestural interactions and non-communicative actions (e.g. Hopkins et al., 2012; Meguerditchian et al., 2013), we expected to find a right-hand bias at the population-level for human-directed gestures but not for conspecific-directed manipulators (prediction n°1).

(2) Does manual laterality vary depending on mechanical effectiveness? To address this question, we distinguished two functions: communication 'requests' (gestures which involve taking into consideration the recipient's response such as TOUCH BODY) and so-called 'manipulators' (mechanically effective social actions used to get things done such as GRAB BODY) used during interactions with conspecifics. Next, we compared the degree of manual laterality involved in both types of signals in relation to three categories of factors previously found to modulate gestural laterality (e.g. Prieur, 2015). These three categories are as follows: interactional context components (visual fields used by both signaller and recipient

during dyadic interactions and associated emotional valence of the context), signal characteristics (e.g. sharing degree[3]) and signaller's socio-demographic characteristics (age, sex, group/zoo, and hierarchy).

It has been hypothesized that actions are deprived of communicative function (e.g. Liebal & Call, 2012; Scott & Pika, 2012) or are less governed by the communication system than gestures that are only used for communicative purposes (Prieur et al., submitted for publication-b). Based on this hypothesis, we predicted that gorillas' conspecific-directed gestures would be more right-lateralised than conspecific-directed manipulators, as for chimpanzees (Prieur et al., submitted for publication-b) (prediction n°2).

(3) Does manual laterality vary depending on recipients' specificity? To investigate this question, we examined manual laterality of gestures directed to conspecifics (conspecific-directed gestures) and to humans (human-directed gestures) in relation to the three categories of factors: interactional context components, signal characteristics, and signaller's socio-demographic characteristics (see question 2 for more details).

Chimpanzees' laterality in both conspecific- and human-directed gestural communications is modulated differently by the recipient's position in the signaller's visual field and by signaller's age (Prieur et al., submitted for publication-b). We assumed that differences would be related, at least in part, to the signaller's emotional state. Indeed, conspecifics' emotional expressions (positive and negative) are probably easier to process than emotional expressions of an other species and this in turn could have a different impact on gestural laterality. Given the phylogenetic closeness between chimpanzees and gorillas (e.g. Kaessmann et al., 2001), we expected our assumption to be true also for gorillas (prediction n°3).

With regards to questions 2 and 3, according to the literature on laterality (e.g. Meguerditchian et al., 2013; Prieur et al., 2016a), we expected modulation of signallers' manual laterality especially by interactional context components (e.g. visual fields of both interactants), sharing degree of signal, and to a lesser extent, individual socio-demographic characteristics (e.g. age and sex).

2. Methods

A detailed description of the subjects and our observational and coding procedure can be found in previous studies (Prieur, 2015; Prieur et al., 2016b). Details are repeated here for the reader's convenience.

2.1. Subjects

Thirty-five lowland gorillas (*Gorilla gorilla gorilla*) raised under semi-natural conditions were observed at three zoos: La Vallée des Singes (France), Apenheul Primate Park and Burgers' Zoo (The Netherlands). The age categories of subjects were based on Breuer, Hockemba, Olejniczak, Parnell, & Stokes' (2009) definitions for infants (0–3 years old), juveniles (4–6 years old) and adolescents (7–11 years old), and on Stoinski, Perdue, Breuer, and Hoff's (2013) categories for young (12–20 years old) and mature (> 20 years old) adults (see Table 1). Our subjects' (23 females and 12 males) ages ranged from 0.5 to 42 years (mean = 13.64; SD = 13.07). For a detailed description of gorillas' housing conditions see Prieur, 2015.

2.2. Observational procedures

Data were collected by J.P. in 2012 at La Vallée des Singes (May 18th–July 25th) and at Apenheul Zoo (August 14th–October 27th) and in 2013 at Burgers' Zoo (April 29th–June 29th), respectively for 196.5 h, 214.5 h and 240 h observation (651 h in all). Data were collected using the behaviour sampling rule "sampling all occurrences of some behaviours" (that consists in recording all occurrences of behaviours of interest in all group subjects during each observation period) with "continuous recording" for the recording rule (Altmann, 1974; Martin & Bateson, 1994). Observation data were collected in real time by using a stopwatch, binoculars, and a paper sheet onto which data were recorded. Data recording was only performed when the subjects were clearly visible. To do so, data were collected mostly from above and as close as possible to the subjects. We maintained a record of the frequency with which a particular individual had been observed. In situations where we could choose which of several dyads to observe, we targeted those individuals previously sampled least often.

Data considered in the present study include:

- a new set of data for the three manipulators (mechanical effective) for 31 of these 35 subjects.
- a new set of data for the five human-directed gesture types for 17 of these 35 subjects.
- a set of data for the eleven conspecific-directed gesture types previously investigated in these 35 subjects from the zoos of La Vallée, Apenheul, and Burgers (Prieur et al., 2016b) for which a new exploitation is made here in the framework of the statistical analysis.

Table 1 presents the repertoire and the detailed description of the 14 frequent intentional signals considered.

2.2.1. General coding procedure of social interactions

We only took into account behaviours produced during dyadic interactions with (a) conspecifics, and (b) humans (i.e. zookeepers and visitors) characterised by the following four key criteria of intentional communication (Bates, Benigni, Bretherton, Camaioni, & Volterra, 1979; Bruner, 1981; Fröhlich et al., 2016; Leavens, Russell, & Hopkins, 2005; Pika & Liebal, 2012): (1) sensitivity to the recipient's attentional state as evidenced by the adjustment of the signaller's communication in relation to the recipient's attention (e.g. emitting a visual signal only when the recipient was looking), (2) waiting for a response as assessed by the signaller pausing (for at least two seconds) while maintaining visual contact with the recipient, (3) signaller's apparent satisfaction as measured by the signaller ceasing communication (i.e. signaller switches to another non-communicative activity (e.g. forage, travel)) when the initial signal was successful as it had achieved its social goal, and (4) signaller's goal persistence as assessed by repetition (i.e. the signaller performs the same type of signal again and/or exaggerates it) and/or elaboration (i.e. the signaller uses a different means of communication by performing another type of signal or a combination of signals) when the initial signal was unsuccessful as it had not achieved its social goal.

We defined the subject that started the social interaction as the signaller and the target of this interaction as the recipient. For each dyadic interaction, we recorded (1) type of signal, (2) limb (hand/foot) used by the signaller to communicate, (3) handedness (left or right hand/foot), (4) interactional context of signal production with the relative positions of both subjects before and during the interaction (visual field and body side), (5) emotional valence of the context (positive or negative) associated with the social interaction (see Section 2.2.3 for further details), and (6) identity and role (signaller or recipient) of both subjects (see Table 1 for further details). The coding procedure associated with each type of signal is described below.

2.2.1.1. Coding procedure for conspecific- and human-directed

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[3] Sharing degree refers to "rare" signals performed by only a few subjects in the population or to "common" signals performed by most subjects in the population.

Table 1
Repertoire and detailed description of intentional signals.

Intentional signal	Description	References
BEAT BODY	Subject slaps once or repetitively (only the hand that slapped first is considered) own body part (except chest) with knuckles or palm of hand	Pika et al. (2003, 2005)
BEAT CHEST	Subject slaps own chest repetitively alternating open hands or knuckles (the hand that slapped first is considered)	Pika et al. (2003, 2005)
CLAP HAND *	One open hand (more often the one in the upper position) strikes against the other hand	Pika et al. (2003, 2005)
SLAP HAND *	Subject hits ground/wall/object with the palm of one hand	Pika et al. (2003, 2005)
EMBRACE	One of signaller's arm is stretched and raised up to about head level with palm facing downwards or placed lightly on the recipient's body	Roth (1995)
CARRY BABY * *(manipulator)*	Subject (usually a mother) holds an infant with one hand and/or one arm while walking (i.e. tripedal carry of infant)	Nishida, Kano, Goodall, McGrew, and Nakamura (1999), Nishida, Zamma, Matsusaka, Inaba, and McGrew (2010)
CRADLE * *(manipulator)*	A mother holds her infant ventrally close to her body with one hand and/or one arm	Nishida et al. (1999, 2010)
EMBRACE HALF	Subject puts one arm around another subject while walking	Nishida et al. (1999, 2010)
EMBRACE LATERAL *	Subject places one arm gently around the other's shoulder, back, or waist, or puts both arms around the other while pulling the recipient closer; both partners are initially side by side and facing the same direction	de Waal (1988)
EMBRACE VENTRAL/DORSAL *	Both arms are opened and the partner is hugged ventro/dorso-ventrally (leading arm recorded), with belly contact	de Waal (1988)
GRAB BODY * *(manipulator)*	Subject grasps the recipient's body (except genitals and lips) with its whole hand, fingers are bent	Pika et al. (2003, 2005)
PUNCH *	Any sort of contact made with fist/wrist or fingers of one hand with another subject, without appreciable force, but the actual contact is more forceful than simply laying hand on another's body	Pollick and de Waal (2007)
TOUCH BODY *	Gentle and brief (< 5 s) contact of the recipient's body (except genitals) with one hand or arm	Pika et al. (2003), Pika et al. (2005)
SHAKE OBJECT *	An object (e.g. branch) is moved back and forth with quick jerky movements of one arm, slightly or vigorously, while the subject is sitting or standing	Kano (1992), Kano (1998)

Intentional signals (eleven gesture types and three manipulators) are grouped by sensory modality (four auditory, eight tactile then 1 visual signals) and arranged according to alphabetic order. Repertoire and details description of gesture types were taken from a previous publication (Prieur et al., 2016b). Signals marked * are followed by descriptions inspired from the mentioned reference(s); they are labelled differently because precisions based on personal observations have been added.

gestures. This study analyses gestures directed towards humans. For comparison, we include the following gestural data sets that have been analysed previously (see Prieur, 2015; Prieur et al., 2016b):

- five gesture types directed towards conspecifics[4] for comparison with human-directed gesture types.
- six gesture types directed towards conspecifics for comparison with conspecific-directed manipulators (see below for further details).

Following Pika's (2008) definition, only behaviours that met the following criteria were classified as gestures: movements of the limbs or head and body that (a) were used to initiate (signaller starts to engage but not continue) a social interaction, (b) were directed towards a particular recipient as shown by signaller's body and/or gaze orientation towards the recipient, and/or physical contact with the recipient, (c) were mechanically ineffective (which means, they were not designed to act as direct physical agents), and (d) elicited a voluntary response by recipients (recipients could choose the behavioural outcome in contrast to mechanical effective behaviours when they are physically manipulated by receivers). When a behaviour did not fulfil criteria (c) and (d) but fulfilled criteria (a) and (b) and the criteria for intentionality (see above), it was classified as a "manipulator" (i.e. mechanical effective social action). Handedness of a given gesture was recorded only during dyadic interactions satisfying the following two conditions: first, both hands of the signaller were free to communicate and, second, they were symmetrically positioned with respect to its body midline before the interaction, without any environmental factors potentially influencing the use of a specific hand (e.g. being close to a wall/bush/tree; Forrester, Quaresmini, Leavens, Spiezio, & Vallortigara, 2012).

Data were recorded for single gestures (defined as gestures followed by a pause of > 1 s waiting for a response, Pika & Liebal, 2012) and for gesture bouts (i.e. gesture sequences[5] separated by a pause of > 1 s) (Marchant & McGrew, 1991). Only the first gesture of a gesture bout sequence was taken into account for further analyses. The following conditions had to be met to consider that a single gesture or a bout was terminated: the signaller's hand returned to its initial position (e.g. Meguerditchian, Vauclair, et al., 2010), switched to another non-communicative activity (e.g. forage, travel), or occurred an incident (e.g. stumble) that could influence the use of one of the hands occurred (e.g. Harrison & Nystrom, 2010). To ensure statistical independence of data (e.g. Morris, Hopkins, & Bolser-Gilmore, 1993), a gesture was recorded as a new gesture event when a change in hand activity lasted more than 3 s (e.g. the signaller ceased to communicate by leaving the location to search for food sources during more than 3 s).

2.2.1.2. Coding procedure for "manipulators".

To enable a quantitative comparison with previously reported intraspecific gestural data (Prieur, 2015; Prieur et al., 2016b), we recorded conspecific-directed mechanically effective actions, so-called "manipulators" during daily activities using the same observational procedure mentioned above for gestures. We only considered so-called 'empty-handed' (Petitto, 1988; Pika, 2008) manipulators of the tactile modality (social actions which are tactile and do not include the use of objects).

2.2.2. Characteristics of intentional signals

Classification of signals (i.e. gesture types and manipulators) was based on previous descriptions (when necessary anatomical elements or precisions were added) (see Tables 1 and 2). In total, we considered eleven gesture types, which we categorised into visual (n = 1), auditory (n = 4) or tactile gestures (n = 6) and three manipulators. To be able to compare this data set of intentional signals to a similar data set on chimpanzees' signal laterality (Prieur et al., submitted for

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[4] The respective physical forms/descriptions of the five gesture types (i.e. BEAT BODY, BEAT CHEST, CLAP HAND, SLAP HAND, and SHAKE OBJECT) are the same independent of the type of recipient (human or conspecific).

[5] Sequences of gestures are series of more than one gesture without interspersed pauses of > 1 s (e.g. Genty & Byrne, 2010).

Table 2
Characteristics, descriptive statistics and analyses of each intentional signal.

Intentional signal	Sensory modality	Sharing degree	N analysed	Data points analysed	Non-lat.	B test lat. vs. non-lat.	LH	RH	B test LH vs. RH	Mean HI	Shapiro test	*t*-test/Wilcoxon test		Mean ABSHI
Conspecific-directed gesture type (n = 35 subjects)														
BEAT CHEST	Auditory	Common	19	1930	5	0.064	4	10	0.180	0.155	0.351	*t* = 1.497	*P* = .152	0.400
BEAT BODY	Auditory	Rare	12	258	9	0.146	0	3	i.l.	0.193	0.759	*t* = 1.533	*P* = .154	0.396
CLAP HAND	Auditory	Rare	17	788	5	0.144	1	11	**0.006**	0.508	**0.003**	W = 141	***P* = .001**	0.678
SLAP HAND	Auditory	Common	22	1710	6	0.053	0	16	**0**	0.530	0.611	*t* = 10.375	***P* < .0001**	0.530
EMBRACE HALF	Tactile	Rare	8	119	7	0.070	1	0	i.l.	−0.021	0.461	*t* = −0.150	*P* = .885	0.271
TOUCH BODY	Tactile	Common	35	2827	29	**0.0001**	2	4	0.688	0.041	**0.020**	W = 349	*P* = .588	0.233
EMBRACE LATERAL	Tactile	Common	21	1020	19	**0.0002**	1	1	i.l.	0.106	0.628	*t* = 2.052	*P* = .053	0.191
EMBRACE	Tactile	Rare	15	325	13	**0.0074**	0	2	i.l.	0.169	0.371	*t* = 2.936	*P* = .011	0.204
EMBRACE VENTRAL/DORSAL	Tactile	Rare	8	81	8	**0.0078**	0	0	i.l.	0.210	0.413	*t* = 1.949	*P* = .092	0.310
PUNCH	Tactile	Common	28	2056	14	1	1	13	**0.002**	0.284	0.588	*t* = 7.098	***P* < .0001**	0.306
SHAKE OBJECT	Visual	Common	20	1539	7	0.263	0	13	**0.0002**	0.299	0.757	*t* = 5.584	***P* < .0001**	0.328
Conspecific-directed manipulator (n = 31 subjects)														
CRADLE	Tactile	Rare	8	2278	1	0.070	7	0	**0.016**	−0.333	0.426	*t* = −12.333	*P* < .0001	0.333
GRAB BODY	Tactile	Common	30	2752	25	**0.0003**	2	3	i.l.	0.092	0.061	*t* = 2.403	*P* = .023	0.184
CARRY BABY	Tactile	Rare	9	2390	3	0.508	4	2	0.688	0.094	0.894	*t* = 0.505	*P* = .627	0.450
Human-directed gesture type (n = 17 subjects)														
BEAT CHEST	Auditory	–	15	477	8	1	3	4	1	**0.046**	0.620	*t* = 0.329	*P* = .747	0.463
BEAT BODY	Auditory	–	5	84	4	i.a.	0	1	i.l.	0.198	0.624	*t* = 1.530	*P* = .201	0.290
CLAP HAND	Auditory	–	12	369	4	0.388	2	6	0.289	0.343	0.046	W = 60	*P* = .110	0.633
SLAP HAND	Auditory	–	10	273	6	0.754	0	4	i.l.	0.460	0.159	*t* = 3.506	***P* = .007**	0.553
SHAKE OBJECT	Visual	–	10	171	8	0.109	0	2	i.l.	0.237	0.865	*t* = 3.438	***P* = .007**	0.266

Intentional signals are grouped by sensory modality and ordered according to increasing HI values. Characteristics, descriptive statistics and analyses for each conspecific-directed gesture type were taken from a previous publication (Prieur et al., 2016b). *N*: number of subjects who performed at least six times each the given gesture; Data points analysed: number data points associated to the N subjects analysed; B test Lat. vs. Non-lat.: p-value of the binomial test performed on the number of lateralised versus non-lateralised subjects; i.a.: insufficient number of subjects analysed for testing; LH: number of left-handed subjects; RH: number of right-handed subjects; B test LH vs. RH: p-value of the binomial test performed on the numbers of left-handed versus right-handed subjects; i.l.: insufficient number of lateralised subjects for testing; Mean HI: Mean Handedness Index score of N analysed subjects, the sign indicates the direction of the signal bias (negative value: left-hand bias, positive value: right-hand bias); *t*-test: *t*-value and p-value of the *t*-test only performed for normally distributed HI values of N analysed subjects; Wilcoxon test: W-value and p-value of the Wilcoxon test performed only when normality of HI values was not verified; Mean ABSHI: Mean Absolute value of Handedness Index score of N analysed subjects. Significant results are depicted in bold.

publication-b), they were classified as follows: “rare signals” and “common signals”. Rare signals (five out of eleven gesture types and two of the three manipulators) were performed by only a few subjects of our study population (performed by < 17 individuals). Common signals (six out of eleven gesture types and one manipulator) were produced by the majority of all individuals observed in the present study.

2.2.3. Characteristics of the interactional context of intentional signal production

We recorded the relative positions – visual field used[6] and exposed body side – of both individuals before (i.e. the last positions in a 2-s time window before the interaction) and during each dyadic interaction. As positions of both subjects before and during an interaction are positively correlated (for more details see Prieur, 2015), we retained only the two following position variables: position of recipient in the signaller’s visual field during the interaction (SVF) and position of signaller in the recipient’s visual field during the interaction (RVF).

Based on Pollick and de Waal’s (2007) and Pika and colleagues’ (2003) definitions, we distinguished two categories of emotional context of interactions: positive and negative. For every interaction/intentional signal, the emotional context was inferred in relation to three criteria: (1) the functional consequences of the signal during the interaction (i.e. recipient’s response to the signaller's signal), (2) the global social context in which the interaction occurred (positive valence: affiliative, food, nurse, play, ride and travel; negative valence: agonistic; see for definitions Pika et al., 2003), and (3) the signaller’s facial and vocal expressions and, to a lesser extent, its whole-body expressions, and pilo-erection (e.g. Schaller, 1963) (see Supplementary Table S1). A signal was classified as positive when it was for instance accompanied by a relaxed facial expression, a vocalisation used only in affiliative contexts (e.g. single grunt) and a global social context of an affiliative nature (e.g. resting).

2.3. Sociodemographic characteristics of the subjects

In addition to gorillas’ individual demographic characteristics, such as age and sex, we took information concerning their genetic relatedness (kin) and their social relationships (affiliation and hierarchy) into account (Prieur, 2015; Prieur, Pika, Barbu, & Blois-Heulin, submitted for publication-c). Details are repeated here for the reader’s convenience.

2.3.1. Kinship

We had permission to use data detailing the genetic relationships of all our subjects. To assess the potential effect of kinship on manual laterality, we considered the three following categories of gorilla pairs: (1) “Parent-infant” including mother-infant and father-infant pairs, (2) “Siblings” including siblings and half-siblings, and (3) “Unrelated” concerning pairs of genetically unrelated subjects.

2.3.2. Affiliation

Following Prieur and colleagues’ (2016a, submitted for publication-c) methodology, we calculated a Dyadic Affiliation Index (DAI) to quantify affiliation based on the relative frequencies of affiliative and

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[6] The visual field used refers to the spatial extent (from 0 to 180°) in which the recipient is located (i.e. in the left or in the right visual field of the signaller). It was termed “enlarged field” by Baraud, Buytet, Bec, and Blois-Heulin (2009).

agonistic behaviours within a dyad. Affiliative and agonistic behaviours were selected based on previous studies of gorillas in the wild (e.g. Harcourt, 1988; Robbins, 1996, 2008) and in captivity (e.g. Genty, Breuer, Hobaiter, & Byrne, 2009; Pika et al., 2003). Considering affiliative behaviours, we selected the following five strictly affiliative gesture types (gestures regularly used and expressed only in positive contexts; 4477 interactions): EMBRACE, EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, and TOUCH BODY. Considering agonistic behaviours, all recorded agonistic interactions (1039) were considered. These interactions included 13 mechanically ineffective gesture types such as KICK (Prieur et al., 2016a, 2016b) and SLAP (Pika et al., 2003; a variant without sufficient force to move recipient's body) as well as two mechanically effective manipulators: GRAB and PUSH (Pika et al., 2003; variants with sufficient force to move recipient's body).

The DAI increases with affinity, and starting from 0 in the absence of affinity (see precise formula in Prieur, 2015). Three categories of dyadic affiliation were considered: (1) "Low" from 0 to 0.5 (335 dyads), (2) "Medium" from 0.5 to 1 (31 dyads), and (3) "High" $>$ 1 (36 dyads).

2.3.3. Hierarchy

Dominance relationships were determined by analysing agonistic interactions (corresponding to moderate and high aggressions defined by Robbins, 2008) when the aggressor and the recipient of a threat could be clearly identified (Langbein & Puppe, 2004). All observed agonistic interactions (1039) fulfilled these criteria and were taken into account. We organised these interactions into socio-metric matrices and analysed them using the MatMan 1.1 programme (Noldus Information Technology, Wageningen, Netherlands). This programme assigns a rank from 1 (the most dominant) to 0 (the most subordinate) to each subject. Three categories of hierarchy were considered: "Subordinate", "Intermediate", and "Dominant" (La Vallée: 6 subordinates, 2 intermediates and 3 dominants; Apenheul: 7 subordinates, 3 intermediates and 4 dominants; Burgers: 4 subordinates, 4 intermediates and 2 dominants). As a linear rank hierarchy could not be established for the gorilla group at La Vallée, their hierarchical categorisation was based on zoo keepers' reports that agreed with the MatMan assessment of hierarchy.

2.4. Statistical analysis

We analysed data for the eleven conspecific-directed gesture types (Prieur, 2015), four human-directed gesture types and three conspecific-directed manipulators (see Tables 1 and 2). All statistical analyses were computed using R programme (version 3.0.3, R Development Core Team, 2014). The level of significance was set at 0.05.

2.4.1. Descriptive statistics of laterality at the individual and population level

We included in the subsequent statistical analyses only those signals (conspecific-directed gestures, human-directed gestures and conspecific-directed manipulators) that fulfilled 1–3 key parameters of intentionality (see method section) and had been recorded at least six times for at least six different subjects (Chapelain, 2010). The only exception was the gesture BEAT BODY, performed by only five subjects. However, we included BEAT BODY in the statistical analyses because it has been described as a typical gesture of Western lowland gorillas (e.g. Genty et al., 2009; Pika et al., 2003). To assess individual-level biases for each signal, we performed the binomial test on the number of responses produced by an individual with its left and right hands. A subject was categorised as lateralised when it presented a significant bias and as non-lateralised when there was no bias. The direction of asymmetry of each individual was evaluated by calculating an individual Handedness Index (HI) using the formula $HI = (R - L)/(R + L)$, where R and L represent the total number of right- and left-hand responses respectively. The strength of individual hand preference was evaluated by the absolute value of HI (ABSHI). This procedure is similar to that used by other researchers (e.g. Harris & Carlson, 1993).

We assessed population-level biases for each signal by comparing the numbers of lateralised and non-lateralised individuals using the binomial test. We assessed population-level biases for only those signals showing laterality in at least six individuals. We compared the numbers of right-handers and left-handers using the binomial test. Considering that laterality varies along a continuum (e.g. Bourne, 2008; McGrew & Marchant, 1997), we evaluated hand use bias at the population level by applying a one-sample two-sided Student's *t*-test on the HI values of all individuals (HI distribution: normal; Shapiro-Wilk normality test). In addition, we used a one-sample Wilcoxon signed rank test when the HI distribution was not normal. Because sample size has been suspected to influence the direction and strength of laterality (McGrew & Marchant, 1997; Palmer, 2002), we used a Spearman correlation test to estimate the potential effect of the number of data points per individual on the direction and strength of laterality.

2.4.2. Generalised linear mixed model analysis of the multiple influential factors

To our knowledge, only Prieur and colleagues (Prieur, 2015; Prieur, Pika, Blois-Heulin, & Barbu, submitted for publication-d; Prieur et al., 2016a, 2017, submitted for publication-b, submitted for publication-c) have previously studied manual laterality:

1. by taking into account simultaneously the potential influence of multiple factors and their interactions (an essential point to avoid biases yielding ambiguous results, and a mandatory requirement to assess particular effects of factors (e.g. mechanical effectiveness));
2. by assessing the effects of three different categories of factors: interactional context components, signal characteristics, and individual sociodemographic characteristics not only of signallers but also of recipients; and
3. by investigating the effects of sociodemographic factors on laterality considering several age categories and dominant status, essential to evaluate the particular effects of each modality of the sociodemographic variables considered.

Multiple predictor variables were considered in the present study (e.g. mechanical effectiveness, emotional context of interaction, signaller's age). We chose signaller's and recipient's identity as random variables depending on the model to prevent pseudo-replication due to repeated observations (Waller, Warmelink, Liebal, Micheletta, & Slocombe, 2013) (see Table 3 for a descriptive summary of dependent, fixed and random variables of each model). We tested to what extent the fixed variables influenced the response variable (signaller's hand use) using generalised linear mixed models (GLMMs; Baayen, 2008) with a binomial error structure and logit link function.

Two GLMMs were considered to assess whether and how (1) function/mechanical effectiveness (Model 1) and communication type (Model 2) impacted subjects' laterality in communicative interactions according to the previously introduced variables/characteristics: intentional signal, interactional context, and individual sociodemographic components. To achieve these goals and to avoid numerical instabilities in the GLMM procedures, we compared right-hand use between categories regrouping particular intentional signals:

– Model 1 compared two categories that involve only the tactile sensory modality without use of an object: one category regrouped the six conspecific-directed gesture types (mechanically ineffective)

Table 3
Generalised linear mixed models 1 and 2 with response, fixed and random variables, description of type and associated levels.

	Name	Type
Model 1	*Response variable*	
	Hand use	Dichotomous (L/R)
	Fixed variables	
	Position of recipient in Signaller's Visual Field during interaction (SVF)	Dichotomous (L/R)
	Position of signaller in Recipient's Visual Field during interaction (RVF)	Dichotomous (L/R)
	Emotional context of interaction	Dichotomous (Negative/Positive)
	Signaller's sex	Dichotomous (F/M)
	Signaller's age	Ordinal (Infant/Juvenile/Adolescent/Young adult/Mature adult)
	Recipient's sex	Dichotomous (F/M)
	Recipient's age	Ordinal (Infant/Juvenile/Adolescent/Young adult/Mature adult)
	Zoo	Nominal (Apenheul/Burgers/La Vallée)
	Signaller's hierarchical rank	Ordinal (Dominant/Intermediate/Subordinate)
	Recipient's hierarchical rank	Ordinal (Dominant/Intermediate/Subordinate)
	Kinship	Nominal (Parent-infant/Siblings/Unrelated)
	Dyadic affiliation index (DAI)	Ordinal (Low/Medium/Strong)
	Sharing degree	Dichotomous (Rare/Common)
	Mechanical effectiveness	Dichotomous (Yes/No)
	Random variables	
	Signaller's identity	Nominal
	Recipient's identity	Nominal
Model 2	*Response variable*	
	Hand use	Dichotomous (L/R)
	Fixed variables	
	SVF	Dichotomous (L/R)
	RVF	Dichotomous (L/R)
	Emotional context of interaction	Dichotomous (Negative/Positive)
	Signaller's sex	Dichotomous (F/M)
	Signaller's age	Ordinal (Infant/Juvenile/Adolescent/Young adult/Mature adult)
	Zoo	Nominal (Apenheul/Burgers/La Vallée)
	Signaller's hierarchical rank	Ordinal (Dominant/Intermediate/Subordinate)
	Recipient's type	Dichotomous (Conspecific/Human being)
	Random variable	
	Signaller's identity	Nominal

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

and the other category regrouped the three conspecific-directed manipulators (mechanically effective). Regrouping the six conspecific-directed gesture types that involve only the tactile sensory modality without use of an object was based on Prieur et al.' (2015, submitted for publication-c) results showing that sensory modality and use of an object while gesturing modulated laterality of gestures.

- Model 2 compared a category of conspecific-directed gesture types and a category of human-directed gesture types (both categories regrouped the same five frequently expressed gesture types: BEAT BODY, BEAT CHEST, CLAP HAND, SLAP HAND and SHAKE OBJECT).

All possible interactions between fixed variables were included in both models at the beginning of the model selection.

The GLMM analyses were performed using the 'glmer' function ['lme4' package (Bates, Maechler, Bolker, & Walker, 2014)]. We selected the best model based on Akaike's information criterion (AIC), by choosing the one with the lowest AIC. We visually checked equivariance, independence and normality of model residuals, using the 'plotresid' function ['RVAideMemoire' package (Hervé, 2014)]. The main effects of the best model were evaluated by type II Wald chi-square tests using the 'Anova' function ['car' package (Fox & Weisberg, 2011]. Least Square means (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") and differences were calculated between LSmeans (lsmeans package).

3. Results

We recorded a total of 7421 manipulators directed towards conspecifics and a total of 1407 gestures directed towards humans. After applying the statistical criterion required for binomial tests (e.g. Prieur et al., 2016b), a total of 7420 conspecific-directed manipulators and a total of 1374 human-directed gestures were retained for the subsequent analyses of manual laterality at the population level. Application of this statistical criterion lead us to consider only the data sets of conspecific-directed manipulators for 31 of our 35 subjects (age distribution: 8 infants, 6 juveniles, 6 adolescents, 6 young adults, 5 mature adults; sex distribution: 20 females and 11 males) and the data sets of human-directed gestures for 17 of our 35 subjects (age distribution: 6 infants, 5 juveniles, 4 adolescents, and 2 young adults; sex distribution: 8 males and 9 females) for subsequent statistical analyses.

3.1. Manual laterality of conspecific-directed manipulators and human-directed gestures at the population level

To evaluate gorillas' manual laterality at the population level, we analysed gorillas' laterality bias for each of the three conspecific-directed manipulators and the five human-directed gesture types (for details see Table 2). For comparison purpose, Table 2 also presents the analyses of manual laterality at the population level for the eleven conspecific-directed gesture types previously assessed by Prieur and colleagues (2015, 2016b). The mean numbers of occurrences per individual were 239.36 for the three manipulators (min = 11, max = 1665; SD = 351.54), and 80.82 for the five human-directed gesture types (min = 7, max = 222; SD = 62.24).

Assessing handedness for conspecific-directed manipulators dichotomously, the results showed that significantly more subjects were non-lateralised concerning the conspecific-directed manipulator GRAB BODY (binomial test: $P = .0003$). The average percentage of non-lateralised subjects for manipulators was 43.06% (min = 12.50%, max = 83.33%, SD = 36.40). Significantly more subjects were left-handed than right-handed for CRADLE (binomial test: $P = .016$). Concerning human-directed gesture types, there was no statistically significant difference between the number of lateralised and non-lateralised subjects (binomial test: $P > .11$). The average percentage of non-lateralised subjects for interspecific gestures was 61.33% (min = 33.33, max = 80%, SD = 19.66).

Assessing handedness for conspecific-directed signals along a continuum, the results showed a significant right-hand bias at the population level for five conspecific-directed gesture types (one-sample two-sided *t*-test and one-sample Wilcoxon signed rank test: $P \leq .011$; Table 2): two auditory (CLAP HAND and SLAP HAND), two tactile (EMBRACE and PUNCH), and one visual gesture types (SHAKE OBJECT). The average Mean HI was 0.23 (min = −0.02, max = 0.53; SD = 0.17) and the average Mean ABSHI was 0.05 (min = 0, max = 0.29; SD = 0.09). We found a significant population-level hand bias towards the left hand for the conspecific-directed manipulator CRADLE and towards the right hand for GRAB BODY (one-sample two-sided *t*-test: $P \leq .023$). The average Mean HI for conspecific-directed manipulators was −0.05 (min = −0.33, max = 0.09; SD = 0.25) and the average Mean ABSHI was 0.06 (min = 0, max = 0.19; SD = 0.11). Concerning human-directed gesture types, we did not find a statistically significant difference between the numbers of right-handed and left-handed individuals (binomial test: $P > .29$). However, there was a significant right-hand bias at the population level for the two human-directed gesture types SLAP HAND and SHAKE OBJECT (one-sample two-sided *t*-test: for both $P = .007$), the average Mean HI was −0.26 (min = −0.05, max = 0.46; SD = 0.16) and the average Mean ABSHI was 0.11 (min = 0.05, max = 0.16; SD = 0.05). There was no significant effect of the number of conspecific-directed manipulator data points per individual on the ABSHI values. However, we found a significant effect on the HI values for CARRY BABY (negative correlation; Spearman correlation test: N = 9, $r_s = -0.71$, $P = .0034$) (see Supplementary Table S2). Furthermore, there was no significant effect of the number of human-directed gesture data points per individual on the HI values, but we found a significant effect on the ABSHI values for SLAP HAND (negative correlation; Spearman correlation test: N = 10, $r_s = -0.64$, $P = .048$). Concerning conspecific-directed gesture types, no significant effect of the number of data points per individual on the HI and ABSHI values was found except for BEAT CHEST (positive correlation for ABSHI; Spearman correlation test: N = 19, $r_s = 0.60$, $P = .007$) and for TOUCH BODY (negative correlation for ABSHI; Spearman correlation test: N = 35, $r_s = -0.44$, $P = .008$) (see Supplementary Table S2).

3.2. Factors and their mutual interactions influencing signal laterality

To investigate whether and how function/mechanical effectiveness (Model 1) and communication type (Model 2) may influence subjects' laterality in signalling activities, we examined two distinct aspects. First, we compared right-hand use between categories of intentional signals:

- Model 1 compared a category regrouping the three conspecific-directed manipulators (34 gorillas and a total of 7421 interactions) and a category regrouping six conspecific-directed gesture types (35 gorillas and a total of 6550 interactions), and
- Model 2 compared a category regrouping five human-directed gesture types (25 gorillas and a total of 1407 interactions) and a category regrouping five conspecific-directed gesture types (31 gorillas and a total of 6297 interactions).

Table 4
Analysis of deviance table (Type II Wald chi-square tests) for models 1 and 2.

Fixed terms and associated interactions	χ^2	*Df*	*P*
Model 1			
Mechanical effectiveness	0.154	1	.695
Signaller's Visual Field during interaction (SVF)	4550.456	1	< 2.2e−16
Recipient's Visual Field during interaction (RVF)	44.529	1	2.506e−11
Emotion	15.578	1	7.916e−05
Sharing degree of gesture	9.415	1	.002
Signaller's age class	15.407	4	.004
Recipient's age class	2.608	4	.625
Signaller's sex	2.489	1	.115
Recipient's sex	4.374	1	**.036502**
Zoo	29.484	2	**3.960e−07**
Signaller's hierarchical rank	6.206	2	**.045**
Affiliation	1.481	2	.477
Kinship	1.672	2	.433
Mechanical effectiveness × Sharing degree of gesture	23.916	1	**1.006e−06**
Mechanical effectiveness × SVF	163.199	1	**< 2.2e−16**
Mechanical effectiveness × RVF	111.754	1	**< 2.2e−16**
Mechanical effectiveness × Signaller's age class	26.910	4	**2.073e−05**
Mechanical effectiveness × Recipient's age class	11.109	4	**.025**
Mechanical effectiveness × Affiliation	6.472	2	**.039**
Mechanical effectiveness × Emotion	6.237	1	**.013**
Model 2			
Gesture directed towards both conspecifics and humans	187.174	4	< 2.2e−16
(SVF)	34.320	1	4.676e−09
(RVF)	0.262	1	.609
Emotion	1.449	1	.229
Signaller's sex	10.845	1	.001
Signaller's age class	183.717	4	< 2.2e−16
Zoo	159.751	2	< 2.2e−16
Signaller's hierarchical rank	98.288	2	< 2.2e−16
Recipient's type	3.224	1	.073
Gesture directed towards both conspecifics and humans × Zoo	116.624	8	**< 2.2e−16**
Gesture directed towards both conspecifics and humans × Signaller's sex	37.752	4	**1.261e−07**
Gesture directed towards both conspecifics and humans × Signaller's hierarchical rank	31.756	8	**.0001**
Gesture directed towards both conspecifics and humans × Emotion	9.126	4	.058
Zoo × Signaller's sex	66.736	2	**3.224e−15**
Zoo × Signaller's hierarchical rank	139.445	4	**< 2.2e−16**
Zoo × Recipient's type	11.406	2	**.003**
Zoo × Emotion	12.647	2	**.002**
Gesture directed towards both conspecifics and humans × (SVF)	11.426	4	**.022**
(SVF) × Signaller's age class	9.758	4	**.045**
Emotion × (RVF)	5.423	1	**.020**

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

Second, we assessed (Model 1 and Model 2) the influence of interactional context, signal, and individual sociodemographic characteristics on right-hand use.

Table 4 presents the analysis of deviance results for the two best GLMM models. In this table, the results corresponding to a given fixed variable (considered separately) have to be ignored when this variable is involved in significant interactions with other variables. In Model 2,

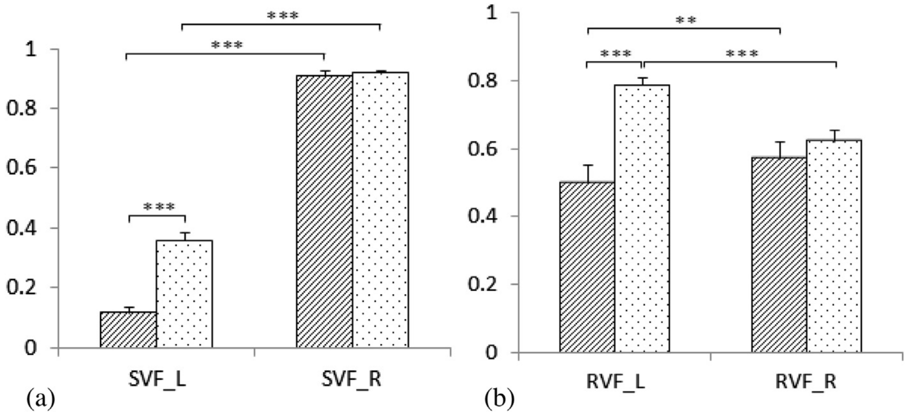

Fig. 1. Right-hand use for manipulators and gestures (adjusted probability ± SE). (a) Interaction with Signaller's Visual Field (SVF): recipient in signaller's left (SVF_L) or right (SVF_R) visual field. (b) Interaction with Recipient's Visual Field (RVF): signaller in recipient's left (RVF_L) or right (RVF_R) visual field (Model 1). Diagonally striped bars: manipulators. Stippled bars: gestures. Tukey test: $^{**}P < .01$, $^{***}P < .001$.

we only considered significant interactions involving "Recipient type" which was the variable of interest. The other variables/interactions introduced in Model 2 were only present to adjust possible effects of "Recipient type" on the dependent variable "Hand use" (see more detailed analyses in Prieur, 2015). Variables for which a significant interaction effect was found were considered successively depending on the model: interactional context variables (signaller's visual field, recipient's visual field and emotional context), signal's characteristic variables (sharing degree, mechanical effectiveness, recipient type) as well as social (kinship, hierarchy, dyadic affiliation) and demographic (age) variables. Results of post hoc multiple comparisons tests for Model 1 (respectively Model 2) are displayed in Appendix Table A1 (respectively Table A2). For clarity, only significant and trend significant p-values of post hoc multiple comparisons tests are mentioned in the text below, but all p-values can be found in Tables A1 and A2.

3.2.1. *Laterality of conspecific-directed manipulators vs. conspecific-directed gestures (Model 1)*

3.2.1.1. Influence of mechanical effectiveness. Signallers were more right-handed when performing gestures (mechanically ineffective) than manipulators (mechanically effective) when the recipient was in the signaller's left visual field (SVF_L Fig. 1a) and when the signaller was in the recipient's left visual field (RVF_L Fig. 1b). Signallers also were more right-handed in negative emotional contexts, and when using rare signals. Infant and mature adult signallers showed a right-hand preference when interacting with a strong affiliative partner and juvenile and adolescent recipients (Tukey test: SVF_L and RVF_L conditions: $P < .0001$; negative emotion: $P = .018$; rare: $P = .0001$; infant signaller: $P = .020$; mature adult signaller: $P = .0009$; strong affiliative partner: $P = .003$; juvenile recipient: $P = .0099$; adolescent recipient: $P = .045$).

3.2.1.2. Influence of interactional context components. The production of gestures and manipulators was more right-lateralised when the recipient was in the signaller's right (SVF_R) than in its left visual field (SVF_L) (Fig. 1a) (Tukey test: $P < .0001$). Furthermore, the production of gestures was more right-lateralised when the signaller was located in the recipient's left (RVF_L) than in its right visual field (RVF_R) (Fig. 1b), and interacted in a negative than in a positive emotional context (RVF_L: $P < .0001$; negative: $P < .0001$). In contrast, the performance of manipulators was more right-lateralised when the signaller was located in the recipient's right (RVF_R) than in its left visual field (RVF_L) ($P = .002$).

3.2.1.3. Influence of signal sharing degree. Common manipulators were more right-lateralised than rare manipulators (Tukey test: $P < .0001$).

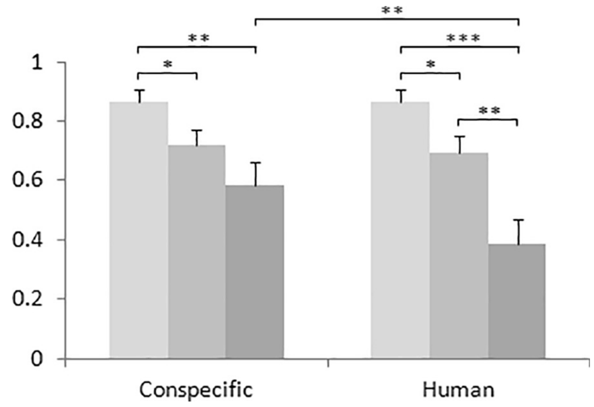

Fig. 2. Right-hand use in relation to signaller's age class (adjusted probability ± SE). Interaction with recipient type (Model 2). Gradual range of grey bars: light grey (Apenheul), grey (Burgers), and dark grey (La Vallée). Tukey test: $^{*}P < .05$, $^{**}P < .01$, $^{***}P < .001$.

3.2.1.4. Influence of individual sociodemographic characteristics. When performing manipulators, infant signallers were found less right-handed than juvenile signallers (Tukey test: $P < .0001$), and juvenile signallers were less right-handed than young adult signallers ($P = .037$). Furthermore, mature adult signallers were less right-handed than juveniles and young adults when performing manipulators (juvenile: $P = .019$; young adult: $P = .002$).

Our results also indicated an influence of recipient's age class and sex on signal laterality: the production of manipulators was more right-lateralised towards juvenile recipients than towards young adult recipients (Tukey test: $P = .037$). Overall, intentional signals (gestures and manipulators) towards male recipients were overall more right-lateralised than intentional signals performed towards female recipients ($P = .037$). In addition, there was an influence of signaller's group on signal laterality: intentional signals were overall more right-lateralised for signallers living in the La Vallée group than individuals living in the Apenheul and Burgers' groups (for both groups: $P < .0001$).

3.2.2. *Laterality in conspecific- vs. human-directed gestures (Model 2)*

3.2.2.1. Influence of recipient type. Conspecific-directed gesture types produced by individuals of the La Vallée group were more right-lateralised than their human-directed gestures (Fig. 2) (Tukey test: $P = .003$).

3.2.2.2. Influence of signaller's group. Individuals of the Apenheul group used their right hands more often to communicate than did individuals living in the Burgers' group whatever the recipient's type (Fig. 2) (Tukey test: conspecific-directed: $P = .031$; human-directed: $P = .022$). The gorillas from Apenheul were also more right-handed when communicating than were gorillas living at La Vallée, whatever the recipient's type (conspecific-directed: $P = .0002$; human-directed: $P < .0001$). Moreover, individuals living in the Burgers' group used their right hands more often than did individuals from the La Vallée group when performing human-directed gestures ($P = .007$).

4. Discussion

The main aim of the present study was to improve our current understanding of gorillas' manual laterality by evaluating the influence of mechanical effectiveness and communication type on their most frequently produced manual signals. We addressed the following three questions: (1) Do gorillas show a right-hand bias at the population-level for conspecific-directed manipulators (mechanically effective) and for human-directed gestures (mechanically ineffective)? (2) Does manual laterality vary depending on mechanical effectiveness? (3) Does manual laterality vary depending on recipients' specificity?

The results showed that consistent population-level hand biases existed along a laterality continuum (e.g. McGrew & Marchant, 1997) for two of the three conspecific-directed manipulators and two of the five human-directed gesture types. Our multifactorial investigation demonstrated that gorilla signallers' manual laterality was influenced by several factors and their mutual intertwinement. Overall, conspecific-directed gestures were more right-lateralised than conspecific-directed manipulators. In addition, we found between-group differences, with gorillas from La Vallée using their right hands more often to produce intentional signals than did individuals living in the two other study groups.

4.1. Manual laterality of intraspecific manipulators and human-directed gestures at the population level

Evaluating laterality along a continuum showed that gorillas were right-handed at the population level for two types of human-directed gesture (SLAP HAND and SHAKE OBJECT) These results are in line with other studies in captivity, providing evidence for population-level right-hand biases when producing human-directed (e.g. chimpanzees: Hopkins et al., 2005; red-capped mangabeys and Campbell's monkeys: Maille, Chapelain, Déruti, Bec, & Blois-Heulin, 2013) as well as conspecific-directed gestures (e.g. chimpanzees: Prieur et al., 2016b; gorillas: Prieur et al., 2016b). Our results support the growing body of work suggesting that primates' cerebral systems processing gestural communication are, at least for some species, right-lateralised.

However, evaluating conspecific-directed manipulators along the laterality continuum showed more heterogeneous results. We found population-level hand biases towards the left for CRADLE and towards the right for GRAB BODY. There was no bias for CARRY BABY. These findings are partly in accordance with our prediction n°1 that gorillas would present a right-hand bias at the population-level for gestural but not for manipulator production. Left-side cradling at the population-level has also been reported for chimpanzees and gorillas (e.g. see Hopkins, 2004 for a review). In addition, our findings support the results of Roger and Kaplan's (1998) study on captive common marmosets (*Callithrix jacchus*, a cooperative breeding species in which both mother and father routinely contribute to the care of their offspring), which did not find a population-level bias for the side of being carried by either mothers or fathers. Interestingly, however mothers of three species of Old World monkeys (Bonnet monkeys, *Macaca radiata*; Japanese macaques, *Macaca fuscata* and Taiwanese monkeys, *Macaca cyclopis*) presented a left-hand preference to pick up a baby in an emergency situation (when mothers were frightened experimentally) (Hatta & Koike, 1991).

Overall, our findings showed that several frequently produced intentional signals in gorillas were biased at the population level, whereas others showed were only weak laterality. In the following paragrahs, we will discuss each of these findings in detail with a special focus on the influence of mechanical effectiveness and communication type on manual laterality and the impact of the three categories of factors previously found to modulate signal laterality (e.g. Prieur, 2015; Prieur et al., 2016a, 2017): interactional context components, signal characteristics and individual sociodemographic characteristics.

4.2. Laterality of conspecific-directed manipulators vs. conspecific-directed tactile gestures

4.2.1. Influence of mechanical effectiveness

We found that gorilla signallers were overall more right-handed when performing conspecific-directed tactile gestures (mechanically ineffective) than conspecific-directed manipulators (mechanically effective). This result is in line with our prediction n°2 concerning the effect of mechanical effectiveness on manual laterality. It also supports with our previous findings concerning the effect of the mechanical effectiveness on laterality in chimpanzees (Prieur et al., submitted for publication-b). We hypothesized that laterality of manipulators (i.e. actions with appreciable force directed towards a social partner) would be less governed by the brain's communication system than laterality of gestures (only used for communication functions). This view is supported by two arguments. First, research has demonstrated that communicative functions in humans (e.g. Corballis, 1991; Knecht et al., 2000) and chimpanzees (e.g. Cantalupo, Pilcher, & Hopkins, 2003; Hopkins, Russell, & Cantalupo, 2007) are predominantly associated with left hemisphere activity leading to predominant use of the right hand. Second, it has been shown that chimpanzees used their right hand more for gesturing (i.e. distinct gesture types: FOOD BEG, POINTING, HAND SLAP, THROWING; a category of three species-typical gesture types combining THREAT, EXTEND ARM and HAND SLAP; a category of five species-typical gesture types involving a communication tool combining DRAG OBJECT, PUT OBJECT ON HEAD/BACK, SHAKE OBJECT, THROW OBJECT and HIT WITH OBJECT) than for non-social manipulations (i.e. tool use, reaching, bimanual coordinated tube task) (Hopkins et al., 2005; Meguerditchian, Vauclair, et al., 2010; Prieur et al., submitted for publication-d). Based on this literature and our findings on gorillas and chimpanzees (Prieur et al., submitted for publication-b), we hypothesized that some primate species may have developed a specific left-hemisphere processing of gestural communication, that is distinct from the cerebral system processing of motor functions of manipulation (not only of an object but also of a conspecific).

4.2.2. Influence of the recipient's position during an interaction

Gorilla signallers showed a right-hand preference for conspecific-directed tactile gestures and conspecific-directed manipulators when recipients were in their right visual fields (SVF_R). This result strengthens previous findings on chimpanzees and gorilla in captivity, which preferentially used their right hands when in SVF_R situations (Prieur et al., 2016a, submitted for publication-b, submitted for publication-c; Prieur et al., 2017). Hence, our results strengthen the argument that signallers use their ipsilateral hand more frequently in those interactions involving a particular gesture category: tactile gestures that require physical contact with a given recipient.

4.2.3. Influence of the signaller's position during an interaction

When producing tactile gestures, gorilla signallers used their right hand more often when they were in the recipient's left (RVF_L) rather than in its right visual field (RVF_R). This finding is in line with recent results on three groups of captive chimpanzees showing that chimpanzee signallers use their right hands more often in RVF_L than in RVF_R situations for tactile gestures (Prieur et al., 2016a, submitted for publication-b). We had hypothesized that a more pronounced recipient's facial expression (via its left hemiface which is more visible for the signaller in RVF_L) would increase the signaller's emotional state and would thus increase the use of its right hand for gestural signalling. Consequently, we assumed that this relationship hypothesized between perception of facial expression and laterality in a communicative context may be shared by gorillas and chimpanzees. This assumption would favour the hypothesis of an evolutionary continuity of brain lateralisation for emotional processing across the primate phylogeny – from Old World monkeys to great apes (e.g. Lindell, 2013).

Gorilla signallers used their right hands for conspecific-directed manipulators more in RVF_L than in RVF_R situations. This result is in contrast to previous findings on chimpanzees (Prieur et al., submitted for publication-b), whose laterality patterns did not differ between these two situations. There are two non-mutually exclusive explanations. First, these differences may be due to differences in methodology by comparing species-typical but non-identical manipulators. As a matter of fact, for the gorilla analysis, we combined the manipulators CRADLE, CARRY BABY, and GRAB BODY, while for the chimpanzee analysis we combined CRADLE, GRAB BODY, GRAB GENITAL, and GRAB LIP. Second, these differences may be the result of differences in social structures and dynamics between the two species as suggested by our previous between-species comparison (Prieur et al., 2017). Gorillas live in polygamous, and generally stable and cohesive groups whereas chimpanzees have less stable social structures since they live in multi-male–multi-female groups characterized by a high degree of fission-fusion dynamics (e.g. Bradley et al., 2004; Goodall, 1986; Mitani, 2009; Schaller, 1963; Watts, 1996). Furthermore, chimpanzees seem to engage in generally lower interindividual distances (Harcourt, 1979; White & Chapman, 1994) than gorillas (Klein, 1999). Chimpanzees' higher degree of interconnection and lower interindividual distances may thus provide greater opportunities for close-range social interactions. Consistent with this hypothesis, Call and Tomasello (2007) showed that captive chimpanzees seem to use a greater proportion of tactile gesture types than captive gorillas. Similarly, chimpanzees may also use (1) a higher proportion of manipulator types (which also imply close proximity) than gorillas and, (2) a higher frequency of tactile gestures and manipulators. Since gorillas may have fewer opportunities to engage in close-range social interactions and seem to be more sensitive to environmental changes and stressful situations (e.g. Masi et al., 2012; Zaragoza, Ibáñez, Mas, Laiglesia, & Anzola, 2011), close-range social interactions could thus increase gorilla signallers' emotional state. An increased emotional state would increase right-hand use as we previously hypothesized. This effect might be particularly important when using manipulators (which imply physical/forceful manipulation of the recipient) that elicit more uncertainty in the recipient's response/reaction compared to gestures.

4.2.4. Influence of emotional context

Our results indicated that gorilla signallers, like chimpanzees, (Prieur et al., submitted for publication-b), used their right hand for conspecific-directed tactile gestures more in negative than in positive contexts. Rohlf and Ramirez's (2006) review of humans' asymmetries suggested that negative emotional states (e.g. anger that generally provokes approach motivation) enhanced activation of the left-prefrontal cerebral hemisphere leading to increased right-hand use in negative emotional contexts. Therefore, this negative valence effect on manual laterality could probably be present in gorillas and chimpanzees – two of humans' closest living relatives. These neurobehavioural processes assumingly shared between chimpanzees, gorillas and humans may be an additional argument supporting the evolutionary continuity of brain laterality traits (e.g. Lindell, 2013; Meguerditchian et al., 2013).

In contrast to the findings on gestures, our results did not indicate any valence effect on laterality of conspecific-directed manipulators. This result is in accordance with our previous results for chimpanzees (Prieur et al., submitted for publication-b). We suggested that in contrast to gestures, laterality of manipulators would not be influenced by the emotional component since manipulators are less governed by the brain's communication system than conspecific-directed gestures.

4.2.5. Influence of signaller's age class

We found an effect of signallers' age class on their right-hand use for conspecific-directed manipulators. Nevertheless, this age effect is ambiguous. Infants were less right-handed than juveniles, which in turn were less right-handed than young adults. These findings are in line with previous studies (e.g. see McGrew & Marchant, 1997 for a review), revealing that direction of primates' hand preference for manipulations becomes more salient with age. Hand preference thus seems to develop during ontogeny and is crucially shaped by practice, learning and experience. However, our study showed that mature adult gorillas were less right-handed than were juveniles and young adults. These results mirror those found in chimpanzees (for both manipulation and intraspecific gestures), with an increase of signallers' right-hand use until adulthood and a decrease in right-hand use by elderly signallers (Prieur et al., 2016a, submitted for publication-d). This possible senescence effect is consistent with the decrease of humans' right-hand use for manipulations with aging (Kalisch, Wilimzig, Kleibel, Tegenthoff, & Dinse, 2006). Possible explanations for this phenomenon are that (1) physical limitations and reduced activity (documented for humans: e.g. Hughes et al., 1997) decrease practice-based performance of the right hand triggering an increase of left-hand use, and/or (2) lower frequencies of social interactions observed in our older gorilla subjects may induce a shift towards ambidexterity with increasing age.

In stark contrast, we did not find any influence of signaller's age class on their right-hand use for conspecific-directed tactile gestures. This finding is in line with a previous report showing that gorilla signallers' age class only influenced laterality of auditory intraspecific gestures but not laterality of tactile and visual gestures (Prieur, 2015).

4.2.6. Influence of recipient's sex

Concerning the impact of sex on laterality of tactile signal production, we found that signallers were more right-handed towards male than female recipients. It may be possible that this result is due to the interaction between sex and dominance status in gorillas. More males (50%) than females (22%) were dominants, and proportionally more females (48%) than males (33%) were classified as subordinate subjects. Interacting with a male is therefore also more stressful than interacting with a female, resulting in a right-side bias use (chimpanzees: Prieur et al., 2016a, submitted for publication-d; gorillas: Prieur et al., 2017; Prieur et al., submitted for publication-c; rats: e.g. Castellano, Diaz-Palarea, Barroso, & Rodriguez, 1989; anoles: Deckel, 1998). This hypothesis is supported by several human studies (see Rohlfs & Ramirez, 2006 for a review), offering an explanation why also gorilla signallers use their right hands more often to perform tactile signals towards a male than towards a female.

4.2.7. Influence of signaller's group

Our results showed that signallers of the La Vallée gorilla group were more right-handed than signallers of the Apenheul and Burgers groups. Interestingly, Prieur and colleagues (submitted for publication-c) found that individuals living in the Apenheul and Burgers groups were overall more right-handed than La Vallée signallers (considering the 16 frequently expressed gesture types). Variations of intentional signal laterality between different groups, which were never in contact with each other, may thus be modulated by the signal characteristics considered (sensory modality and mechanical effectiveness). In addition, they may also be highly influenced by interactional context components (emotional context) and/or signallers' sociodemographic characteristics (hierarchy and sex) (Prieur et al., 2016a, submitted for publication-c). Possible causes of such variations/modulations between different groups could also be genetic and/or social factors and learning possibilities. For instance, genetic and social factors have been commonly used to explain differences of laterality patterns between social groups for chimpanzees (probing task: Hopkins, Reamer, Mareno, & Schapiro, 2015; attention getting sounds: Taglialatela, Reamer, Schapiro, & Hopkins, 2012) and humans (e.g. see Fagard, 2013 for a review).

4.3. Laterality of conspecific- vs. human-directed gestures

4.3.1. Influence of recipient type

La Vallée signallers were more right-handed when producing conspecific-directed gestures than human-directed gestures. To our knowledge, this is the first evidence of a direct difference in gestural laterality between conspecific- and human-directed gestures. This result supports our prediction n°3, stating that gestural laterality between conspecific- and human-directed gestures may be related to the signallers' emotional state: conspecifics' emotional expression might be easier to process than non-conspecifics' emotional expressions that could, in turn, impact/increase signallers' emotional state. As previously hypothesized, this increased emotional state could increase gorilla signallers' right hand use. The present finding thus also strenghtens our previous findings on chimpanzees' laterality, showing that both conspecific- and human-directed gestures were modulated differently by the position of the recipient in the signaller's visual field and by the signaller's age (Prieur et al., submitted for publication-b).

4.3.2. Influence of signallers' group

Signallers from the Apenheul group were more right-handed when performing gestures than Burgers and La Vallée signallers regardless of the recipient type (conspecific or human). Furthermore, individuals living in the Burgers' group were more right-handed than La Vallée signallers when producing human-directed gestures. As stated above, genetic and/or social learning factors may explain the between-group differences of gestural laterality.

5. Conclusions

Here, we provide evidence for population-level laterality in gorillas for two conspecific-directed manipulators and two human-directed gesture types. The application of the multifactorial approach was crucial to explain differences in laterality patterns between the three activity types: conspecific-directed manipulators, human-directed gestures, and conspecific-directed gestures. Overall, our study showed that conspecific-directed gestures were more right-lateralised than conspecific-directed manipulators. Moreover, it indicated that gorillas of one study group used their right hand more frequently to produce conspecific-directed gestures than human-directed gestures. In sum, these findings support the hypothesis that laterality of gestural communication is a relevant functional marker of the left-brain specialisation for language (e.g. Corballis, 2002; Meguerditchian & Vauclair, 2000; Prieur et al., submitted for publication-b). We suggest that some primate species have a specific left-hemisphere system processing of gestural communication, which is distinct from the cerebral system processing of motor functions of manipulation (not only of an object but also of a conspecific). Future research should expand this unprecedented multifactorial approach onto carefully chosen representatives of the more than 50 genera of primates, to enable us to map out cladistically the evolution of primates' laterality and impact of social systems and matrices (Prieur et al., submitted for publication-e). Furthermore, it is important to investigate whether communicative complexity and laterality of distinct communicative signals are interlinked (Pika, 2017).

Statement of significance to the neurobiology of language

Our study supports the evolutionary continuity theory of brain lateralisation for communication by focusing on gorillas, one of our closest living primate relatives. Applying an unprecedented methodological design and presenting newest findings on great ape laterality, we hope to significantly influence the thoughts and ideas of researchers working on the neurobiology of language and the evolution of communicative signalling.

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Appendix A

See Tables A1 and A2.

Table A1
Results of post hoc multiple comparisons tests for model 1.

	Contrast			Estimate	SE	z.ratio	P
Model 1	*Zoo*						
	Apenheul	–	Burgers	0.141	0.100	1.404	.339
	Apenheul	–	La Vallée	−0.380	0.087	−4.350	< **.0001**
	Burgers	–	La Vallée	−0.520	0.106	−4.924	< **.0001**
	Recipient's sex						
	F	–	M	−0.130	0.062	−2.091	**.037**
	Signaller's hierarchical rank						
	Dominant	–	Intermediate	0.163	0.119	1.367	.358
	Dominant	–	Subordinate	−0.066	0.150	−0.441	.899
	Intermediate	–	Subordinate	−0.229	0.104	−2.205	.070
	Mechanical effectiveness × Sharing degree						
	No,Common	–	Yes,Common	0.286	0.225	1.270	.582
	No,Common	–	No,Rare	−0.033	0.110	−0.303	.990
	Yes,Common	–	Yes,Rare	0.911	0.158	5.768	< **.0001**
	No,Rare	–	Yes,Rare	1.231	0.288	4.275	**.0001**
	Mechanical effectiveness × SVF						
	No,R	–	Yes,R	0.078	0.248	0.315	.989
	No,R	–	No,L	2.988	0.069	43.313	< **.0001**
	Yes,R	–	Yes,L	4.349	0.081	53.434	< **.0001**
	No,L	–	Yes,L	1.439	0.243	5.920	< **.0001**
	Mechanical effectiveness × RVF						
	No,R	–	Yes,R	0.212	0.244	0.868	.821
	No,R	–	No,L	−0.809	0.068	−11.959	< **.0001**
	Yes,R	–	Yes,L	0.285	0.078	3.637	**.002**
	No,L	–	Yes,L	1.305	0.247	5.288	< **.0001**
	Mechanical effectiveness × Signaller's age class						
	No,Ado.	–	Yes,Ado.	0.689	0.270	2.555	.240
	No,Ado.	–	No,Inf.	0.212	0.142	1.497	.894
	No,Ado.	–	No,Juv.	0.118	0.118	0.994	.993
	No,Ado.	–	No,M.adu.	−0.186	0.264	−0.705	1.000
	No,Ado.	–	No,Y.adu.	0.067	0.167	0.404	1.000
	Yes,Ado.	–	Yes,Inf.	0.499	0.205	2.440	.302
	Yes,Ado.	–	Yes,Juv.	−0.371	0.191	−1.944	.639
	Yes,Ado.	–	Yes,M.adu.	0.536	0.185	2.891	.108
	Yes,Ado.	–	Yes,Y.adu.	−0.108	0.154	−0.702	1.000
	No,Inf.	–	Yes,Inf.	0.976	0.283	3.446	**.020**
	No,Inf.	–	No,Juv.	−0.095	0.097	−0.975	.994
	No,Inf.	–	No,M.adu.	−0.399	0.289	−1.378	.934
	No,Inf.	–	No,Y.adu.	−0.145	0.209	−0.693	1.000
	Yes,Inf.	–	Yes,Juv.	−0.870	0.174	−4.986	< **.0001**
	Yes,Inf.	–	Yes,M.adu.	0.037	0.271	0.136	1.000
	Yes,Inf.	–	Yes,Y.adu.	−0.607	0.241	−2.517	.259
	No,Juv.	–	Yes,Juv.	0.201	0.282	0.714	.999
	No,Juv.	–	No,M.adu.	−0.304	0.279	−1.089	.986
	No,Juv.	–	No,Y.adu.	−0.050	0.180	−0.278	1.000
	Yes,Juv.	–	Yes,M.adu.	0.907	0.261	3.468	**.019**
	Yes,Juv.	–	Yes,Y.adu.	0.263	0.211	1.243	.965
	No,M.adu.	–	Yes,M.adu.	1.411	0.333	4.240	**.001**
	No,M.adu.	–	No,Y.adu.	0.254	0.254	0.997	.993
	Yes,M.adu.	–	Yes,Y.adu.	−0.644	0.158	−4.075	**.002**
	No,Y.adu.	–	Yes,Y.adu.	0.514	0.259	1.980	.613
	Mechanical effectiveness × Recipient's age class						
	No,Ado.	–	Yes,Ado.	0.861	0.269	3.199	**.045**
	No,Ado.	–	No,Inf.	0.098	0.106	0.922	.996
	No,Ado.	–	No,Juv.	0.091	0.098	0.922	.996
	No,Ado.	–	No,M.adu.	0.020	0.201	0.098	1.000
	No,Ado.	–	No,Y.adu.	0.192	0.129	1.488	.898
	Yes,Ado.	–	Yes,Inf.	0.003	0.183	0.015	1.000
	Yes,Ado.	–	Yes,Juv.	0.252	0.184	1.372	.936
	Yes,Ado.	–	Yes,M.adu.	0.050	0.241	0.209	1.000
	Yes,Ado.	–	Yes,Y.adu.	−0.417	0.203	−2.055	.560
	No,Inf.	–	Yes,Inf.	0.766	0.255	3.002	.080
	No,Inf.	–	No,Juv.	−0.007	0.098	−0.074	1.000
	No,Inf.	–	No,M.adu.	−0.078	0.207	−0.378	1.000
	No,Inf.	–	No,Y.adu.	0.094	0.146	0.644	1.000
	Yes,Inf.	–	Yes,Juv.	0.250	0.186	1.343	.944
	Yes,Inf.	–	Yes,M.adu.	0.048	0.249	0.191	1.000
	Yes,Inf.	–	Yes,Y.adu.	−0.420	0.205	−2.044	.568
	No,Juv.	–	Yes,Juv.	1.022	0.280	3.650	**.010**
	No,Juv.	–	No,M.adu.	−0.071	0.210	−0.338	1.000

(*continued on next page*)

Table A1 (*continued*)

	Contrast			Estimate	SE	z.ratio	P
	No,Juv.	–	No,Y.adu.	0.101	0.130	0.782	.999
	Yes,Juv.	–	Yes,M.adu.	−0.202	0.268	−0.754	.999
	Yes,Juv.	–	Yes,Y.adu.	−0.669	0.205	−3.264	**.037**
	No,M.adu.	–	Yes,M.adu.	0.891	0.355	2.513	.262
	No,M.adu.	–	No,Y.adu.	0.172	0.211	0.815	.998
	Yes,M.adu.	–	Yes,Y.adu.	−0.467	0.274	−1.708	.792
	No,Y.adu.	–	Yes,Y.adu.	0.252	0.285	0.884	.997
	Mechanical effectiveness × Affiliation						
	No,Strong	–	Yes,Strong	0.990	0.266	3.716	**.003**
	No,Strong	–	No,Low	0.225	0.098	2.295	.196
	No,Strong	–	No,Medium	0.077	0.099	0.778	.971
	Yes,Strong	–	Yes,Low	−0.162	0.121	−1.345	.760
	Yes,Strong	–	Yes,Medium	−0.230	0.139	−1.653	.563
	No,Low	–	Yes,Low	0.602	0.243	2.483	.129
	No,Low	–	No,Medium	−0.149	0.117	−1.266	.804
	Yes,Low	–	Yes,Medium	−0.068	0.119	−0.573	.993
	No,Medium	–	Yes,Medium	0.683	0.263	2.595	.099
	Mechanical effectiveness × Emotion						
	No,N	–	Yes,N	1.324	0.451	2.933	**.018**
	No,N	–	No,P	1.116	0.239	4.668	< **.0001**
	Yes,N	–	Yes,P	−0.015	0.390	−0.039	1.000
	No,P	–	Yes,P	0.193	0.117	1.645	.353

L: Left; R: Right; Imm.: Immature; Ado.: Adolescent; Y.adu.: Young adult; M.adu.: Mature adult; Eld.: Elder; P: Positive; N: Negative; estimate: difference between LSmeans SE: Standard Error of the difference; z.ratio: ratio of the estimate to its standard error; *P*: Tukey's p-value. Significant results are depicted in bold.

Table A2
Results of post hoc multiple comparisons tests for model 2.

Model 2	Contrast			Estimate	SE	z.ratio	*P*
	Signaller's age class × Recipient's type						
	Apenheul,Conspecific	–	Burgers,Conspecific	0.909	0.302	3.011	**.031**
	Apenheul,Conspecific	–	La Vallée,Conspecific	1.501	0.396	3.791	**.002**
	Apenheul,Conspecific	–	Apenheul,Human	0.005	0.098	0.054	1.000
	Burgers,Conspecific	–	La Vallée,Conspecific	0.592	0.305	1.938	.379
	Burgers,Conspecific	–	Burgers,Human	0.115	0.121	0.952	.933
	La Vallée,Conspecific	–	La Vallée,Human	0.821	0.221	3.707	**.003**
	Apenheul,Human	–	Burgers,Human	1.019	0.326	3.127	**.022**
	Apenheul,Human	–	La Vallée,Human	2.317	0.448	5.173	< **.0001**
	Burgers,Human	–	La Vallée,Human	1.298	0.372	3.486	**.007**

L: Left; R: Right; Imm.: Immature; Ado.: Adolescent; Y.adu.: Young adult; M.adu.: Mature adult; Eld.: Elder; P: Positive; N: Negative; estimate: difference between LSmeans SE: Standard Error of the difference; z.ratio: ratio of the estimate to its standard error; *P*: Tukey's p-value. Significant results are depicted in bold.

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandl.2017.10.001.

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