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Chimpanzees' and gorillas' intraspecific gestural laterality:

a multifactorial investigation

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Forward

The human brain was first documented to be asymetrically structured for language related functions (Broca 1865). Since Broca's pioneering discovery, accumulated literature revealed human cerebral laterality for motor, sensory, cognitive and emotional functions (e.g. Hugdahl & Davidson 2002). Among them, handedness has been one of the most investigated features.

Modern humans present a strong preference for right-hand use for manipulation activities at the population level (e.g. Hécaen & de Ajuriaguerra 1964; McManus 1991). 90% of humans preferentially use their right hand for complex tasks such as writing, bimanual coordinated actions and tool use (e.g. Annett 1985; Fagard 2004; Faurie 2004; Faurie & Raymond 2004). However, reports evidence geographical frequency variations in the number of right- and left-handed humans (e.g. Coren & Porac 1977; Perelle & Erhman 1994; Marchant et al. 1995; Marchant & McGrew 1998; Faurie 2004; Faurie & Raymond 2004; Raymond & Pontier 2004). For instance, Perelle and Erhman (1994) showed that the proportions of left-handed individuals in 17 countries ranged from 2.5 to 12.8% for writing. Prehistoric evidence based on fossil and archeological data (e.g. Cashmore et al. 2008; Uomini 2009) showed that Neanderthals also exhibited a robust right-hand preference. Studies of skeletal asymmetries indicate that older hominid species (i.e. *Australopithecus* and early *Homo*) also showed a right-hand preference at the population level (Uomini 2009).

A right-hand preference by humans has been evidenced for gestures. In the present PhD thesis, the term "gesture" is restricted to communication functions and defined as "movements of the limbs or head and body directed towards a recipient that are goal-directed, mechanically ineffective (that is, they are not designed to act as direct physical agents) and receive a voluntary response" (Pika & Bugnyar 2011; p 4). Reports concern gestures accompanying speech (e.g. Dalby et al. 1980, Kimura 1973a, 1973b; Saucier & Elias 2001) and sign language by deaf adult speakers (e.g. Bellugi 1991; Corina et al. 1992; Grossi et al. 1996; Vaid et al. 1989) as well as gestures produced from early infancy on such as POINTING[1] and/or symbolic gestures (e.g. Bates et al. 1986; Blake 2000; Cochet & Vauclair 2010a, 2010b; Vauclair & Imbault 2009; Young et al. 1985). In addition, humans' gestural communication involves brain regions similar to those processing spoken language (i.e. Broca and Wernicke's areas) (e.g. Horwitz et al. 2003; Xu et al. 2009). Interestingly, about 95% of right-handed and between 70 and 85% of left-handed humans for manipulation present a

[1]From here, gestures are written in lower capitals

predominance of the left hemisphere of the brain for language (Knecht et al. 2000; Perlaki et al. 2013). This predominance in a majority of left-handers was also verified by other authors (Pujol et al. 1999; Tzourio et al. 1998).

The ontogenetic and phylogenetic mechanisms which lead to this overexpression of right-hand use by humans are still difficult to understand despite the growing and substantial body of research. Studies suggested a genetic basis of human handedness by providing evidence of the heritability pattern of this trait such as a familial history with a high rate of left-handed individuals (e.g. Annett 1973; Llaurens et al. 2009; Medland et al. 2010), and a higher concordance of handedness between monozygotic than dizygotic twin (McManus & Bryden 1992; Sicotte et al. 1999). Adoption studies also evidenced that the a child's handedness is more strongly related to that of its biological than its adoption parents (Hicks & Kinsbourne 1976; Carter-Saltzman 1980).

However reports show that environmental factors can modulate human handedness. First, evidence for an environmental basis of human lateralization is based on developmental factors in prenatal and postnatal environments. Several studies suggest that lateralized behaviour would be present in the early intrauterine developmental stage. For instance, fetuses present a right-side bias when beginning to move one arm at 9-10 weeks (Hepper et al. 1998), sucking their thumb from 15 weeks of gestation (Hepper et al. 1991), and turning their head relative to their body from 35 weeks of gestation (Ververs et al. 1994). Prenatal exposure to high levels of testosterone has been suspected to play a role in the development of left-handedness (e.g. Geschwind & Galaburda 1985a–c). Indeed, male fetuses exposed to higher levels of prenatal testosterone than female fetuses present a slowdown in neuron growth in certain regions of the left cerebral hemisphere resulting in an increase of left-hand use (Geschwind & Behan 1982; Geschwind & Galaburda 1987). Concerning the postnatal environment, longitudinal investigations of newborns evidence a head position effect hypothesized to contribute to the development of handedness (e.g. Michel 1981; Konishi et al. 1987). For example, newborn infants who preferentially directed their head towards the right at birth (Churchill et al. 1962; Goodwin & Michell 1981) and at 3 to 8 weeks of age (Michel 1981) were more likely to use later more their right hand than their left hand to reach and to grasp objects.

Second, cultural factors influence handedness (e.g. see review Llaurens et al. 2009; Schaasfma et al. 2009). As a matter of fact, social pressures can change hand used for some activities such as forced right-handedness evidenced in several countries for writing (e.g. France: Dellatolas et al. 1988; Finland: Vuoksimaa et al. 2009; Germany: Siebner et al. 2002)

and food-related activities (e.g. Ivory Coast and Sudan: De Agostini et al. 1997; Japan: Shimizu & Endo 1983; Tunisia: Fagard & Dahmen 2004).

As concluded by Fagard (2013) in her review, the combination of genetic factors (potentially influencing motor and postural asymmetries) as well as biological and cultural environmental factors occurring at different periods during development could explain handedness. In addition, gestures (e.g. signing and pointing), known to influence the development of language (Iverson & Goldin-Meadow 2005), could lead to a greater degree of young children's right-handedness than non-communication actions (Bates et al. 1986; Bonvillian et al. 1997; Vauclair & Imbault 2009; Cochet & Vauclair 2010b; Cochet et al. 2011; Meunier et al. 2012; Esseily et al. 2011; Jacquet et al. 2012). This could be related to relatively independent developments of hand preference for communication and non-communication functions (Jacquet et al. 2012). To our knowledge, as yet only Cochet and colleagues (2012) investigated this issue in human adults. They evidenced greater right-hand use in bimanual manipulation actions than in POINTING produced without speech and an absence of significant differences in the direction of laterality between bimanual manipulation actions and POINTING produced with speech. Currently, the results of such comparative approach of humans' manual laterality between communication and non-communication functions remain unclear and further investigations are needed.

Altogether, these studies showed the predominant involvement of humans' left cerebral hemisphere in processing non-communication and communication activities but also evidenced the ambiguous relationship between the direction of handedness for manipulations and lateralization of language. These findings have thus raised the following questions:

Did our ancestors' gestural communication contribute to the emergence of the left-hemisphere language specialization of modern humans? Are manual actions performed in contexts in which manipulation and gestural communication occur[2] controlled by different lateralized cerebral structures?

From an evolutionary point of view, studying the behavioural asymmetries of other animal species should help to understand better laterality of humans' manipulation and gestural communication.

[2] From here, we refer to manipulation as manual actions deprived of communication function

CHAPTER 1

Introduction

1. Brain lateralization: a widespread phenomenon

Recent studies suggest that brain laterality is more ancient than previously expected (Vallortigara et al. 1999; Vallortigara 2006; MacNeilage et al. 2009). Brain and behaviour laterality at the population level, once thought to be specific to humans, has been evidenced in all vertebrate classes (i.e. fish: Sovrano et al. 1999; amphibians: Robins et al. 1998; reptiles: Deckel 1995; birds: Vallortigara 1992; and mammals: Casperd & Dunbar 1996; for a recent review, see Rogers et al. 2013) and several phyla of invertebrates (insects: Letzkus et al. 2006; arachnids: Heuts & Lambrechts 1999; malacostracans: Takeuchi et al. 2008, gastropods: Matsuo et al. 2010; cephalopods: Jozet-Alves et al. 2012; and nematodes: Hobert et al. 2002; for reviews, see Frasnelli 2013; Frasnelli et al. 2012a). The apparent ubiquity of brain lateralization phenomenon in the animal kingdom suggests that from an evolutionary point of view, it would contribute significantly to biological fitness.

The related limb asymmetry has been extensively documented among vertebrates. However, although growing and substantial body of research, the phylogenetic mechanisms which lead to the overexpression of right-hand use in humans are still difficult to understand. Indeed, if humans have been shown to exhibit a strong right-hand preference at the population level (e.g. McManus 2002), non-human limb preference is not so obvious depending on the species. Ströckens and colleagues (2013) have shown in their review that among 119 animal species, 61 (51.3%) exhibited a population-level bias, 20 (16.8%), exhibited individual-level biases and 38 (31.9%) did not show evidence of laterality.

According to the theory of the evolution of laterality at the population level (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009), brain lateralization may have evolved in two steps. First, biases at the individual level would have been selected because it would improve cognitive abilities by avoiding replication of functions and hemispheric competition (e.g. Corballis 1989; Bisazza et al. 1998) and by allowing simultaneous processing of different sources of information (e.g. Rogers 2002; Rogers et al. 2004). For instance, researchers have compared the performance of lateralized and non-lateralized individuals and have shown that lateralization improves behavioural efficiency (e.g. fishes for spatial orientation: Sovrano et al. 2005; birds for foraging and vigilance against predators: Rogers 2000, 2002; Rogers et al. 2004; cats for catching: Fabre-Thorpe et al. 1993; non-human primates for foraging: Fragaszy & Mitchell 1990; McGrew & Marchant 1992, 1999; Butler et al. 1995; Hopkins et al. 2002; Hopkins & Russell 2004). Second, biases at the population level (i.e. populations including unequal numbers of left- and

right-lateralized subjects) could have emerged from an Evolutionarily Stable Strategy (ESS)/frequency-dependent selection based on interspecific prey-predator interactions. This would have created advantages by coordinating behaviours of asymmetric organisms, but also disadvantages by making behaviours more predictable for predators and prey (e.g. shoaling fish: Vallortigara & Bisazza 2002). Ghirlanda and colleagues (2009) proposed however that the pattern of population-level laterality could be explained by an ESS based on a trade-off between competitive and cooperative intraspecific interactions better than by interspecific interactions. Social laterality could have appeared at the population level through social pressures (Vallortigara & Rogers 2005) and because it facilitated intraspecific interactions (Rogers 2000). This facilitation of intraspecific interactions has been evidenced for invertebrates (e.g. spitting spiders: Ades & Ramires 2002; Heuts et al. 2003; red wood ants: Frasnelli et al. 2012b; fiddler crabs: Backwell et al. 2007) as well as for lower vertebrates (e.g. fish: Bisazza et al. 1999, 2000; amphibians: Robins et al. 1998, Vallortigara et al. 1998; birds: Vallortigara et al. 2001; Ventolini et al. 2005) and higher vertebrates (e.g. ungulates: Versace et al. 2007, Jennings 2012; cetaceans: Karenina et al. 2010, 2013; primates: Baraud et al. 2009, Meguerditchian et al. 2010a). For example, Baraud and colleagues (2009) showed that social rank influenced mangabeys' approach side as well as relative transversal and vertical positions. As a matter of fact, high-ranking subjects were approached more often from their left than from their right. Furthermore, they put in evidence that high-ranking subjects were more likely to leave other group members behind them than lower-ranking ones. The latter were found to commonly remain below other group members. Knowing that facial expressions of emotions are more pronounced on the left than on the right hemiface (e.g. humans: Nicholls et al. 2002; chimpanzees: Wallez et al. 2012; rhesus macaques: Hauser 1993; baboons: Wallez & Vauclair 2011), Baraud and colleagues hypothesized that mangabey subjects exhibiting such social laterality bias could take advantage "by approaching a dominant group member by its left and/or frontally, as they can then pay more attention to its left-facial expressions or to all its face or body, in order to improve its perception and to anticipate its reactions, thereby maybe avoiding brutal and/or inappropriate reactions" p. 456. This is consistent with recent findings on children', chimpanzees' and gorillas' social laterality (Quaresmini et al. 2014; Forrester et al. 2014). All the above-mentioned findings have emphasized the importance of studying laterality not only in interspecific interactions but also in intraspecific ones. Moreover, studies are necessary (1) to check whether population-level laterality could arise from social pressures and (2) to identify which factors (e.g. hierarchical rank) could be involved in such social pressures.

Despite all substantial scientific advances into the investigation of laterality of limb use and laterality in social behaviour, further studies are needed for a better understanding of the evolutionary origins of populational right-handedness and of left-cerebral lateralization for language in humans. To this end, non-human primates and particularly great apes can provide particularly valuable clues (e.g. Corballis 2002; Mac Neilage 1984; Vauclair et al. 1999; Hopkins 2007; Meguerditchian et al. 2013).

2. Relevance of non-human primates as model to study the evolutionary origins of language

Non-human primates are the closest phylogenetic species to humans (e.g. Langergraber et al. 2012; Scally et al. 2012). Moreover, they show remarkable resemblance to humans in terms of hand anatomy (e.g. Aiello & Dean 1990; Napier 1962) and ability to manipulate (e.g. Byrne et al. 2001; Napier 1960) as well as in terms of neuroanatomical brain asymmetries (e.g. Cantalupo & Hopkins 2001; Gannon et al. 1998; Hopkins et al. 2007). Studies both in captivity and in the wild have also reported that certain non-human primates are able to make and use tool: chimpanzees (e.g. Gruber et al. 2010; McGrew & Marchant 1992), bonobos (e.g. Roffman et al. 2015; Kano 1982), gorillas (e.g. Lonsdorf et al. 2009; Grueter et al. 2013), orangutans (e.g. Nakamichi 2004; Van Schaik et al. 2003), and capuchins (e.g. Lavallee 1999; Perry et al. 2003). Non-human primates are also relevant models to help us explore the origins of human language. Three main theories have been put forward to explain the emergence of human language: the vocal theory, the gestural theory and the multimodal theory.

1) The theory of vocal origin states that calls would represent a precursor of human language (e.g. Masataka 2003; Seyfarth 1987; Snowdon 2009; Zuberbühler et al. 2009; Lemasson 2011). Indeed several key characteristics of human language are also found in non-human primates' vocalizations of which primitive forms of:

- semanticity or referentiality as evidenced by alarm calls conveying particular semantic content with respect to the type of predators (e.g. Seyfarth & Cheney 2003) or the nature of the food encountered by conspecifics (e.g. Slocombe & Zuberbühler 2005),
- syntax as showed by calls which could be combined into sequences of calls emitted in predatory context or not (e.g. Clarke et al. 2006; Arnold & Zuberbühler 2006),

- conversation-like properties such as turn-taking with callers awaiting another individual's response before calling again (e.g. Snowdon & Cleveland 1984; Sugiura & Masataka 1995),
- flexibility in acoustic structure with evidence of acoustic divergences between population or groups (e.g. Green 1975; de La Torre & Slocombe 2009) as well as acoustic variations according to the caller's hierarchical rank (Fisher et al. 2004) and the group composition and social relationships between group members (e.g. Lemasson et al. 2003; Maciej et al. 2013),
- flexibility in comprehension as some species have been shown to respond distinctively to vocalizations according to information they convey (e.g. Vervet monkeys: Seyfarth et al. 1980; Cheney & Seyfarth 1981; Campbell's monkeys: Zuberbuhler 2001),
- flexibility to social audience as observed for food calls of cotton-top tamarins (Roush & Snowdon 2000), for alarm calls of Thomas-langur (Wich & Sterck 2003) with individuals producing more vocalizations when conspecifics are present than absent as well as for agonistic screams of chimpanzees (Slocombe & Zuberbühler 2007) with individuals modifying their vocalizations in the presence of individuals who could potentially aid them (i.e. individuals that were equal or higher hierarchical ranking to the chimpanzee aggressor).

The evidence of turn-taking (i.e. response-waiting) and such manifestations of flexibility in non-human primates' vocal communication would thus suggest a certain form of intentionality in their vocalizations.

2) Gestural laterality of non-human primates and particularly our closest living relatives, the great apes, is the focus of an ever-growing body of research (e.g. Shafer 1987; Marchant & McGrew 1996; McGrew & Marchant 1997; Hopkins et al. 2012; Meguerditchian et al. 2013). These studies have nurtured recent scientific debates on the origins of language by providing arguments in favour of its gestural origin (Arbib et al. 2008; Corballis 2002, 2003; McNeill 2012).

A first argument supporting the gestural theory of language origin is that non-human primates' gestural communication is more flexible in learning and use compared to non-human primates' vocalizations (e.g. Call & Tomasello 2007; Meguerditchian & Vauclair 2008). Indeed, it is very flexible according to the social context, the individuals' social rank and age (e.g. Maestripieri 1999; Call & Tomasello 2007; Pika et al. 2005a; Pika 2008a; Arbib et al. 2008; Hobaiter & Byrne 2011) leading to large variations of the composition, morphology and size of the gestural repertoire between individuals and groups of a given species. On the contrary, there is less variation of the composition and size of the vocal repertoire between individuals and groups of a given species (e.g. Meguerditchian & Vauclair

2014). For example, the use of certain species-typical gestures is restricted to particular age classes in chimpanzees (Hobaiter & Byrne's 2011b). Interestingly, older subjects are more likely to use the most effective gestures (i.e. gestures producing the desired goals), and the number of gesture sequences[3] they used decreased as well as their gestural repertoire with age. These findings thus provided additional support to previous studies of apes revealing that adults use a smaller gestural repertoire than juveniles (e.g. Tomasello et al. 1985, 1989, 1994; Call & Tomasello 2007). The apparent flexibility of learning and use of non-human primates' gestural communication seems to be due to three complementary mechanisms: phylogenetic ritualization[4], ontogenetic ritualization[5] and social learning (e.g. Tinbergen 1952; Tomasello et al. 1997; Call & Tomasello 2007; Arbib et al. 2008; Liebal & Call 2012).

A second argument is provided by the recent discovery of monkeys' and humans' so-called mirror neurons that presumably exist in all primate brains (see review: Fabbri-Destro & Rizzolatti 2008). As shown by Gallese and colleagues (1996) for rhesus monkeys, mirror neurons are neurons that discharge both when a subject performs a given action and when it observes the same action being performed by the experimenter. More recently, it has been shown that mirror neurons could also be activated when the monkey hears the related sound of the given action (Kohler et al. 2002) as well as when observing actions involving the use of tools (Ferrari et al. 2005) and communicative mouth actions both performed by a human social partner (Ferrari et al. 2003). These mirror neurons involved in the production and the perception of visuo-gestural actions and of oro-facial communication are located in area F5, which is homologous to humans' language production area (e.g. Nishitani & Hari 2000). Furthermore, the study of hemispheric specialization for communication shows a predominance, in humans' left cerebral hemisphere, of Broca's area (responsible for speech production) and Wernicke's area (responsible for understanding speech) (Horwitz et al. 2003; Xu et al. 2009) and of homologous areas in great apes (Gannon et al. 1998; Cantalupo & Hopkins 2001; Hopkins & Nir 2010). Correlatively, observations of apes in captivity revealed

[3] Hobaiter and Byrne (2011b) defined a sequence of gestures as "a series of more than one gesture without interspersed pauses of >1 s, the criterion used by Genty and Byrne (2010)" p. 829.

[4] Liebal and Call (2012) explained that phylogenetic ritualization is a process based on the assumption that communicative displays (e.g. dominance signals such as mounting) would have emerged from body movements lacking communicative goal because "borrowed" from other contexts (e.g. sexual context).

[5] Arbib and colleagues (2008) explained that ontogenetic ritualization is a process based on the assumption that a communicative signal "is created by two individuals shaping each other's behavior in repeated instances of an interaction over time. For example, play hitting is an important part of the rough-and-tumble play of chimpanzees, and many individuals come to use a stylized "arm-raise" to indicate that they are about to hit the other and thus initiate play (Tomasello et al. 1997)" p. 1058.

that gestures were expressed mainly via the right hand (e.g. Hopkins et al. 2012). According to some studies, non-human primates' vocal communication would seem more closely tied to a given emotional control because spontaneous vocal production might not be governed by cortical structures (motor cortex and homologous areas of human language) unlike human language and the gestural communication of chimpanzees and baboons (Aitken 1981; Ploog 1981; Preuschoft & Chivers 1993; Wiesendanger 1999; Meguerditchian & Vauclair 2014; but see also Coudé et al. 2011 and Hage & Nieder 2013 for controversial results).

A third argument stresses the deep intertwinement between humans' spoken language and gesture laterality with a predominant use of the right hand for (i) speech-accompanying gestures (e.g. Kimura 1973a; Saucier & Elias 2001), (ii) sign language by deaf speakers (e.g. Bellugi 1991; Corina et al. 1992) and (iii) pre-linguistic gestures in children (e.g. Blake 2000; Vauclair & Imbault 2009).

A fourth argument in favour of the gestural origin of language is that non-human primates' gestural communication system shares several key characteristics with human language (detailed in 3.1) such as intentionality (e.g. Call & Tomasello 2007; Meguerditchian & Vauclair 2006; Meunier et al. 2013a; Maille et al. 2012; Bourjade et al. 2014) and referential properties (e.g. imperative POINTING: Leavens & Hopkins 1999; DIRECTED SCRATCHES: Pika & Mitani 2006; BECKONING: Genty & Zuberbühler 2014). All these properties underlying the production and use of sophisticated gestural communication are crucial prerequisites for human language.

3) As mentioned above, several key properties of human language have been described in the complex systems of gestural and vocal communications leading researchers to propose an alternative and modern theory. There is a rapidly growing number of recent studies claiming for the theory of a multimodal origin of language: the gestural and vocal origins of human language would not be mutually exclusive (e.g. Arbib et al. 2008; Masataka 2008; Meguerditchian et al. 2011; Lemasson 2011; Slocombe et al. 2011; Tagliatella et al. 2011; Meguerditchian & Vauclair 2014). This is in agreement with studies of humans (e.g. Bernardis et al. 2008; Gentilucci et al. 2008; Xu et al. 2009) suggesting that both speech and gestures would be under control of a common integrated communication system located in the left cerebral hemisphere. This theory of a multimodal origin of language emphasizes the necessity to investigate the evolutionary roots of human language by applying an approach taking simultaneously into account as much as possible the collective knowledge discovered

from different areas of investigation of which those related to the study of laterality in non-human primates gestural communication.

3. Non-human primates' handedness

3.1. Gestural communication in non-human primates

Here, we present a brief overview of studies focusing on gestural communication in non-human primates. These studies have considered many species including great apes (chimpanzees: e.g. Tomasello et al. 1985; Goodall 1986; Pika & Mitani 2006; bonobos: e.g. de Waal 1988; Pika et al. 2005a; Genty & Zuberbühler 2014; gorillas: e.g. Tanner & Byrne 1999; Pika et al. 2003; Genty et al. 2009; orangutans: e.g. Call & Tomasello 1994; Liebal et al. 2006; Cartmill & Byrne 2010), lesser apes (white-handed gibbons: Baldwin & Teleki 1976; siamangs: Fox 1977; Liebal et al. 2004a), olive baboons (Meguerditchian & Vauclair 2006; Meguerditchian et al. 2011; Meunier et al. 2012), mandrills (Laidre 2008, 2011) and several macaques species (e.g. Maestripieri 1997, 1999; Hesler & Fisher 2007) (see also review Call & Tomasello 2007).

Many studies in captivity and in the wild have reported a complex and flexible gestural communication system of non-human primates and especially of great apes (e.g. Call & Tomasello 2007; Cartmill & Byrne 2007, 2010; Genty et al. 2009; Hobaiter & Byrne 2011; Kalan & Rainey 2009; Leavens et al. 2004, 2005; Liebal et al. 2004b, 2004c, 2006; Pollick & de Waal 2007). First, the size of their gestural repertoire is considerable and exhibit a great variety of gestures (e.g. chimpanzees: Nishida et al. 1999, 2010; bonobos: De Waal, 1988; Pika et al. 2005a; gorillas: Pika et al. 2003; Genty et al. 2009; orangutans: Liebal et al. 2006; see also Call & Tomasello 2007 and Pollick & de Waal 2007). Considering the total gestural repertoire of each of the four great apes as well as siamangs and Barbary macaques found across different studies, Call and Tomasello (2007) reviewed that at least 50 percent of each species' repertoire was constituted by manual gestures with the highest proportion (73%) found in gorillas. Their repertoire was constituted by visual gestures (that generate a mainly visual component with no physical contact such as ARM RAISE and EXTEND HAND), tactile gestures (that include physical contact with the recipient such as EMBRACE and TOUCH BODY), auditory gestures (that generate sound while being performed such as SLAP HAND and BEAT BODY) and object manipulation gestures (that involve the use of an object such as SHAKE OBJECT and THROW OBJECT).

Second, non-human primate species can produce intentional gestures. These gestures performed by a signaller 1) must serve to reach a social goal, 2) are directed towards a particular recipient as evidenced by body orientation, gaze alternation and/or physical contact with the recipient, 3) are expected to produce a response from the recipient indicated with gazing at the recipient, and/or communicative persistence in case the recipient did not react or the recipient's response did not match the signaler's goal (e.g. chimpanzees: Tomasello et al. 1989; Leavens et al. 2004; bonobos: Pika et al. 2005a; gorillas: Pika et al. 2003; Genty et al. 2009; orangutans: Cartmill & Byrne 2010; olive baboons: Meguerditchian & Vauclair 2006; Meunier et al. 2013a; Tonkean macaques: Meunier et al. 2013b; red-capped mangabeys and Campbell's monkeys: Maille et al. 2013a; see also Pollick & De Waal 2007 and Call & Tomasello 2007).

Third, gestures of non-human primates are also characterized by flexibility of use (e.g. chimpanzees: Goodall 1968; Liebal et al. 2004b; Hobaiter & Byrne 2011; bonobos: Pika & Tomasello 2002; Pika et al. 2005a; gorillas: Pika & Tomasello 2002; Pika et al. 2003; Genty et al. 2009, 2010; orangutans: Liebal et al. 2006; squirrel monkeys: Anderson et al. 2001, 2007, 2010; see also Pollick & de Waal 2007 and Call & Tomasello 2007). For instance, it has been shown that chimpanzees can use a particular gesture in different functional contexts (e.g. play, aggression, appeasement, food, sex, nursing, and grooming) and a single functional context may elicit diverse gestures (e.g. Goodall 1968, 1986; Hobaiter & Byrne 2011; Roberts et al. 2012a; Tomasello et al. 1994, 1997). It has also been established that all great apes species can invent or individually learn new gestures (i.e. idiosyncratic gestures used only by single individuals among a group) in captivity (e.g. chimpanzees: Tomasello et al. 1997; bonobos Pika et al. 2005a; gorillas; Pika et al. 2003; orangutans: Liebal et al. 2006) and also in the wild for chimpanzees (Goodall 1986; Roberts et al. 2014).

Fourth, literature put in evidence that non-human primates and particularly all the four great apes adjust their gestural communication to the attentional state of the recipient, such that the signaller gestures more to a recipient oriented towards itself and/or use adequate type of gesture (e.g. chimpanzees: Liebal et al. 2004b; Leavens et al. 2005; gorillas: Liebal et al. 2004c; Genty et al. 2009; orangutans: Cartmill & Byrne 2007, 2010; tufted capuchin monkeys: Hattori et al. 2010; squirrel monkeys: Anderson et al. 2010; red-capped mangabeys: Maille et al. 2012; see also Call & Tomasello 2007). For example, visual gestures are mainly performed when the recipient is looking at the signaller whereas auditory gestures less so and tactile gestures are performed independently of the audience's attention (Call & Tomasello 2007; Tanner & Byrne 1996). Based on results of experimental studies (Bräuer et al. 2005;

Okamoto-Barth et al. 2006; Liebal et al. 2004c), Call and Tomasello (2007) noted that chimpanzees and bonobos may be more particularly sensitive to audience effect than gorillas and orangutans. Non-human primates and noticeably great apes are thus particularly relevant models to explore the phylogeny of hemispheric lateralization related to gestural communication in the perspective of the evolutionary contributions of gestures to the emergence of human language. To date, numerous studies and reviews have dealt with manual laterality in non-human primates (by 29th June 2015, Google Scholar search results indicated a total number of 11300 research articles dealing with "manual laterality in non-human primates"). From this literature emerged several hypotheses about the evolutionary origins of human handedness and several important issues which are addressed below.

3.2. Manual laterality in non-human primates: hypotheses on the origins of human handedness and important issues.

3.2.1. Hypotheses about the evolutionary origins of human manual laterality

Four major hypotheses have been suggested to explain the origins of human manual asymmetry:

1) The *postural origins hypothesis* (MacNeilage et al. 1987; MacNeilage 2007) stipulates that primate manual laterality would be the product of structural and functional adaptations for feeding. These would have emerged in two steps. Firstly, left-hand preference would have appeared for visually guided unimanual reaching to predate (e.g. fruit manipulation) while the right hand would have been used for stability of posture and arboreal locomotion. Secondly, the evolution towards terrestrial locomotion in primates may have allowed them to be free from postural restriction associated with arboreal lifestyle and consequently their right hand to become specialized for tasks with certain level of demand such as bimanual manipulation. This hypothesis is supported by studies of arboreal species (orangutans: Hopkins et al. 2011; gibbons: Olson et al. 1990; siamangs: Morino 2011; Redmond 2004; snub-nosed monkeys: Zhao et al. 2010; De Brazza's monkeys: Schweitzer et al. 2007; prosimians: Papademetriou et al. 2005) as well as of more terrestrial species (gorillas, bonobos and chimpanzees: Hopkins et al. 2011; baboons: Vauclair et al. 2005; rhesus macaques: Bennett et al. 2008). On the contrary, this hypothesis is not fully supported by some other studies (e.g. reviews McGrew & Marchant 1997; Papademetriou et al. 2005) mainly on prosimian behaviors. Indeed, as far as we know, there is no evidence of right-hemisphere predominance (i.e. left-hand preference) in prosimians for visual spatial processing. This apparent contradiction would suggest that

lateralization of hand function in primates might have emerged later than previously thought, maybe around the split between the *strepsirrhines* and the *haplorhines* about 55 million years ago (Dodson et al. 1992; Falk 2000; Scheumann et al. 2011). The postural origins hypothesis suggests a task complexity effect leading to right-hand use only at certain level of demand which is in line with the three hypotheses mentioned below.

2) The *artefactual hypothesis* argues that manual laterality of non-human primates would be the product of experimental (Warren 1980) and/or environmental factors related to captivity (McGrew & Marchant 1997; McGrew & Marchant 2001; Palmer 2003). According to Warren (1980), learning through induced practice (e.g. experimental device) would elicit stronger laterality than spontaneous daily actions (e.g. simple reaching to pick up food from the floor). This assumption has been supported by studies in non-human primates (e.g. Chapelain et al. 2006; Fagot & Vauclair 1991; Fragaszy & Adams-Curtis 1993; McGrew & Marchant 1997; Schweitzer et al. 2007; Trouillard & Blois-Heulin 2005). For instance, Chapelain and colleagues (2006) investigating manual laterality in Campbell's monkeys have shown that subjects were less lateralized to perform spontaneous daily actions (e.g. "hold a food item" and "take food out from mouth") than experimental tasks (e.g. simple reach tasks with variation of postural demands and the "box task"[6]). Furthermore, these authors evidenced that the simplest task as well as the category combining the spontaneous actions tended to induce the weakest laterality. According to McGrew and Marchant (1997, 2001) and Palmer (2003), human-rearing during infancy, artificial captive conditions and environmental stress would influence manual laterality in non-human primates, namely captive individuals would be more right-handed than wild ones. As a matter of fact, some studies have found a human-rearing influence on manual laterality in non-communication actions (chimpanzees: Hopkins et al. 1993; Hopkins 1994) and in gestures (chimpanzees: Hopkins 1999; Hopkins & Cantero 2003). However, a growing body of evidence has not found a significant effect of rearing history on laterality in non-communication actions (e.g. chimpanzees: Hopkins 1995; Hopkins & Rabinowitz 1997; Hopkins et al. 2003, 2004; Llorente et al. 2010; bonobos: Chapelain 2010), in gestures (e.g. chimpanzees: Hopkins & Leavens 1998; Hopkins & Wesley 2002; Hopkins et al. 2005a 2005b; Fletcher 2006) and in both non-communication actions and

[6] The "box task" is an experimental task first introduced by Quiatt and Derr (1994) to study hand preference for coordinated bimanual actions. In this task, the subject has to take a seed out of a box previously kept closed with a lid, the box being attached onto the wire-net inside its cage. To do so, the subject has to open the lid and keep it open with one hand while taking the seed out with the other hand.

gestures (pooled data) (e.g. chimpanzees: Fletcher & Weghorst 2005). Moreover, no effect of communication target (intraspecific versus human-directed gestures: Meguerditchian & Vauclair 2006; Meguerditchian et al. 2010a, 2011) on captive chimpanzees' gestural communication has been evidenced. Taking into consideration these findings, we argue that population-level handedness in non-human primates communication is not a consequence of captive environment and human presence. Differences in laterality pattern between results found in captive and wild environmental conditions might rather be due to methodological differences such as the type of behaviour considered to examine hand preference (Hopkins 1999; Hopkins & Cantalupo 2004) and by the nature of the task (e.g. Rogers 2009). Indeed, as we will see with the following hypothesis considering the task complexity, the existence and strength of manual laterality vary greatly with the nature of the manipulative activity.

3) The *task complexity hypothesis* proposed by Fagot and Vauclair (1991) predicts an absence of laterality (an ambidextrous pattern) in tasks requiring low level of manipulatory requirement (i.e. involving a single act such as reaching) and a stronger hand preference in tasks requiring high level of manipulatory requirement (i.e. involving multiple acts such as bimanual coordinated actions and tasks with complementary role differentiation). In accordance with this hypothesis, many studies have put in evidence that complex bimanual behaviours elicit significant right-hand bias at the population level in chimpanzees (in the wild: Lonsdorf et al. 2005; in captivity: Hopkins 1995; Hopkins et al. 2003, 2004, 2011; Llorente et al. 2011), gorillas (in the wild: Byrne & Byrne 1991; in captivity: Hopkins et al. 2011; Meguerditchian et al. 2010b), captive olive baboons (Vauclair et al. 2005) as well as in human infants (Potier et al. 2013) and adults (Cochet & Vauclair 2012; Marchant et al. 1995). More generally, the expression of right-handedness has been shown to be positively correlated to increased complexity of manipulative activities:

- within unimanual actions (e.g. simple food reaching task vs. wadge-dipping in chimpanzees: Boesch 1991; comparisons between brachiating, and bipedal and tripedal standing to reach food in red-capped mangabeys: Blois-Heulin et al. 2006; small vs. large food items to "grasp" in Tonkean macaques: Canteloup et al. 2013),

- between unimanual and bimanual coordinated actions (e.g. simple food reaching task vs. the coordinated bimanual "tube task"[7] in baboons: Vauclair et al. 2005; the "box without lid task"[8] (which require a simple unimanual action) vs. the "box task" in Campbell's monkeys: Chapelain et al. 2006).

Therefore, it has been proposed that laterality for complex tasks particularly those requiring a precision grip such as tool-use would have served as a preadaptation for the appearance of left-hemispheric lateralization for motor functions and language in humans (e.g. Frost 1980; Bradshaw & Rogers 1993; Greenfield 1991; Breuer et al. 2005; Hopkins et al. 2007; Gonzales & Goodale 2009; Uomini 2009; Forrester et al. 2013). This has led several researchers to lay the hypothesis that tool-use *per se* would have played a crucial role in the emergence of human-right-handedness.

4) The *tool use hypothesis* postulates that the strong predominance of right-hand use in humans is a characteristic developed through tool use that was already present in the common ancestor shared by 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 having showed that right-handed actions are associated to the left-cerebral hemisphere ability of dealing with complex temporal sequences of motor activities required for tool making and use (Foucart et al. 2005; Weiss & Newport 2006; Mercader et al. 2007). Language capability would thus have emerged as an extension of this left cerebral hemisphere ability. This hypothesis is supported by brain imaging studies which showed: first the evidence of left-hemispheric anatomical specialization of language areas homologs in great apes (Gannon et al. 1998; Cantalupo & Hopkins 2001; Hopkins & Nir 2010) known to make and use tool (e.g. chimpanzees: McGrew 1992; bonobos: Kano 1982; gorillas: Grueter et al. 2013; orangutans: Van Schaik et al. 2003; second the evidence that asymmetries in the homologs of the human Broca's and Wernicke's areas are associated with handedness for tool use in chimpanzees (Hopkins et al. 2007); third the overlap of brain activity for perceiving language and using

[7] The "tube task" is an experimental task first introduced by Hopkins (1995) to study hand preference for coordinated bimanual actions. In this task, the subject has to hold a baited tube with one hand and extract the food inside the tube with a finger of the other hand.

[8] The "box without lid task" is an experimental task first introduced by Chapelain and colleagues (2006) to study hand preference for unimanual actions. In this task, the subject has to take a seed out of an open box attached onto the wire-net inside its cage.

tools in Broca's area (Higuchi et al. 2009). Throughout these hypotheses, we can see that posture, task complexity and tool-use are factors which have likely influenced the evolution of manual asymmetry in primates. However, it must be noted that complementary factors (e.g. interactional context, gesture types and individual sociodemographic characteristics) have been found to modulate manual laterality and thus have to be considered to avoid erroneous results and/or interpretation as well as inconsistencies between studies.

3.2.2. Factors modulating manual laterality

The non-human primate literature on handedness put in evidence that many complementary factors could modulate manual laterality in both non-communication actions and gestures in its direction, strength and/or consistency (both within and across subjects and both within and across tasks) in non-human primate species of which New World and Old World monkeys as well as Great apes (e.g. see reviews McGrew & Marchant 1997; Meguerditchian et al. 2013). Among these factors, we can mention as follows: individual sociodemographic characteristics (age, sex, group, kinship and hierarchy), then context-related characteristics (position of the target, emotional context), and gesture type.

1) Individual demographic characteristics (age, sex, and group)

These characteristics have been typically the first ones to be examined with, however, heterogeneous results among studies. With regards to age, many studies in non-communication actions (i.e. manipulations) (e.g. chimpanzees: Boesch 1991; Hopkins 1994, 1995; Humle & Matsuzawa 2009; bonobos: Chapelain & Hogervorst 2009; Chapelain et al. 2011; Hopkins et al. 1993; Hopkins & de Waal 1995; orangutans: Rogers & Kaplan, 1996; capuchin monkeys: Westergaard & Suomi 1993, 1994; lemurs: Ward et al. 1990; bushbabies: Milliken et al. 1991; marmosets: Hook & Rogers 2000) and in gestures (e.g. chimpanzees: Hobaiter & Byrne 2013; Hopkins & Leavens 1998; olive baboons: Meguerditchian & Vauclair 2006), have found that direction and/or strength of hand preference becomes more salient with age suggesting that hand preference may be under control of maturation and/or the result of the amount of practice, learning and experience. However, age effects have not been consistently found across studies either in non-communication actions (e.g. chimpanzees: Hopkins 1993; Colell et al. 1995; bonobos: Colell et al. 1995; gorillas: Meguerditchian et al. 2010b; olive baboons: Fagot et al. 1988; Vauclair & Fagot 1987; Meguerditchian & Vauclair 2009; rhesus monkeys Fagot et al. 1991; capuchin monkeys: Parr

et al. 1997; tamarins: Diamond & McGrew 1995) or in gestures (e.g. chimpanzees: Hopkins et al. 2005b; olive baboons: Meguerditchian & Vauclair 2009), making difficult to draw firm conclusions about age.

Sex has also been shown to influence manual laterality with higher left-hand preference in males compared to females in non-communication actions (e.g. chimpanzees: Byrne & Corp 2003; Corp & Byrne 2004; Hopkins et al. 2009; orangutans: Rogers & Kaplan 1996; De Brazza's monkeys: Schweitzer et al. 2007; squirrel monkeys: Meguerditchian et al. 2012a; capuchin monkeys: Meunier & Vauclair 2007; Phillips & Sherwood 2007; Spinozzi et al. 1998; bushbabies: Milliken et al. 1991; see also Sommer & Kahn 2009 for a review). As far as we know, only two studies have detected a sex effect in gestures with however opposite results. Indeed, Hopkins and Leavens (1998) found in chimpanzees that males tended to be less right-handed than females whereas Hopkins and de Wall (1995) found in bonobos that males were more right-handed than females. Nevertheless, some other authors did not find sex differences in manual laterality either in non-communication actions (e.g. chimpanzees: Hopkins 1995; gorillas: Meguerditchian et al. 2010b; olive baboons: Meguerditchian & Vauclair 2009, lemurs: Leliveld et al. 2008, see also reviews of Hook-Costigan & Rogers 1997; McGrew & Marchant 1997) or in gestures (e.g. chimpanzees: Hopkins et al. 2005a, 2005b; Meguerditchian et al. 2010a; olive baboons: Meguerditchian & Vauclair 2006, 2009), remaining open the issue of the influence of sex on laterality.

The influence of belonging to a group and group differences in laterality has also been considered in some previous studies. Indeed, the social hypothesis of laterality (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009) has postulated that social pressures may lead to the alignment of the direction of laterality at the group[9] level in social behaviours. Concerning non-social behaviours (e.g. manipulations using a tool), Lonsdorf and Hopkins (2005) have suggested that an effect of genetic factors and/or social learning on laterality would explain variation of laterality pattern between groups. Concerning this group effect, previous studies have not shown however any significant difference in hand preference between groups of captive chimpanzees (for the "tube task": e.g. Hopkins et al. 2004; for human-directed FOOD BEG: Hopkins et al. 2005a; for human-directed CLAPPING: Meguerditchian et al. 2012; for THROWING directed towards both humans and conspecifics (pooled data): Hopkins et al. 2005b) and baboons (for HAND SLAP directed towards both humans and conspecifics (pooled data): Meguerditchian et al. 2011). It is

[9] 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).

nevertheless of importance to continue the efforts in comparing different groups to get a better understanding of underlying mechanisms of population biases in laterality.

2) Individual social characteristics (kin, hierarchical and affiliative relationships within groups)

Contrary to the individual demographic characteristics, the effect of the individual social ones on manual laterality has been much less documented. Some studies have put in evidence a kinship effect on hand preference in non-communication actions (chimpanzees: Hopkins 1999, Hopkins et al. 2000, 2001a; see also review Teichroeb 1999). Hopkins (1999) has suggested that the direction of hand preference for the coordinated bimanual tube task in chimpanzees is heritable without involvement of the mechanism of genetic transmission. This author mentioned that "there are at least three possible environmental, experiential, or biological factors that may account for the heritability of direction in hand preference in chimpanzees, including (a) maternal cradling bias (Provins 1997), (b) intrauterine fetal position (Previc 1991), or (c) prenatal hormonal environment (Geschwind & Galaburda 1985a)" p. 6. Strong evidence is still needed to support or to contradict any of these possible explanations. By contrast, several studies did not detect such kinship effect in non-communication actions (e.g. Chapelain 2010; Hook & Rogers 2000; McGrew & Marchant 1992; Vauclair & Fagot 1987) and in both non-communication actions and gestures (pooled data) (chimpanzees: Hopkins et al. 2005b).

As far as we know, no study has investigated hierarchical rank effects on manual laterality. However, it must be noted that such effects have already been addressed on visual laterality in the study of Baraud and colleagues (2009). They showed that rank influenced mangabeys' approach side as well as relative transversal and vertical positions: high-ranking subjects were approached more often from their left than from their right. To our knowledge, the influence of affiliation on laterality remains undocumented. Given the potential effects of the individual social characteristics kinship and hierarchical rank on social laterality, we could suspect that relationship quality within dyads would also modulate laterality.

3) Context-related characteristics (position and nature of the target as well as emotional context)

The positions effect of the target (food item to grasp or social partner to communicate with) has been the focus of recent studies. With respect to the sagittal positioning of the item to grasp, several studies have investigated hand preferences in non-communication actions by

the mean of the "QHP task"[10]. The authors have shown that hand preferences of baboons (Meunier et al. 2011; Bourjade et al. 2013), Tonkean macaques (Meunier et al. 2013b), capuchin monkeys (Meunier et al. 2013c) as well as Campbell's monkeys and red-capped mangabeys (Chapelain et al. 2012; Maille et al. 2013a) depend on the item's position. Indeed, subjects strongly preferred to use their ipsilateral hand (i.e. the hand that was closest to the item) for grasping the item. Concerning the distal positioning of the item to grasp, using the same QHP task as mentioned above and varying the distance (close or far) of the food item with respect to the tested subjects, Maille and colleagues (2013) have shown that Campbell's monkeys and red-capped mangabeys use their ipsilateral hand for grasping actions requiring low-arm extension whereas they use their contralateral hand (i.e. the hand that was farthest to the item) for grasping actions requiring full-arm extension. Surprisingly, relatively little is known in gestures about the impact of the position of the target on primates' hand preference. To date, Hopkins and Wesley (2002) have reported an influence of the experimenter's position on hand use for FOOD BEG and POINTING (pooled data) by chimpanzees (Hopkins & Wesley 2002) with subjects using more their right hand to perform FOOD BEG than POINTING. However no evidence of an influence of the experimenter's position was found for food-begging tasks in baboons (Bourjade et al. 2013).

The nature of the target to contact physically (animate or inanimate) has been investigated by Forrester and colleagues (2011, 2012, 2013). They found a correlation between handedness and the animate quality of the target in gorillas, chimpanzees, and children using a common methodological technique (i.e. a corpus technique called the multidimensional method (MDM) and developed by Forrester (2008)). For each species, they have shown that unimanual actions directed toward an inanimate target (i.e. objects, ground, and enclosure) were significantly more performed with the right hand whereas no hand preference was found for such actions directed toward an animate target (i.e. conspecific, self). Handedness seems thus to differ between actions directed towards objects or individuals.

To our knowledge, the effect of the emotional valence of the context on non-human primates' gestural laterality has never been investigated. Nevertheless some studies have

[10] The QHP task (i.e. a task for Quantification of Hand Preferences) is an experimental task first introduced by Bishop and colleagues (1996) to study human hand preference. Thereafter, it has been adapted for non-human primates using food items (Meunier et al. 2011; Chapelain et al. 2012). In this task the subject has to grasp a food item previously placed at one of the five possible positions marked on an experimental table which is in front of the subject. Each position is separated from the adjacent position(s) by 30° on a half-circle, at a reachable distance from each subject's hand (e.g. see Meunier et al. 2011 for more explanation about the QHP task).

already addressed this effect on perceptual – auditory and visual – laterality. For instance, Basile and colleagues (2009) showed that only negative voices (defined as conspecific sounds having a negative emotional value) induced an auditory laterality preference towards the right (resp. left) in Campbell's monkeys (resp. human girls). Moreover, intraspecific agonistic interactions have been found to induce a preferential use of the left visual field in baboons (Casperd & Dunbar 1996). Differently, Chapelain and colleagues (in prep.) found a left visual field bias for bonobos' positive interactions. These studies highlight complex interactions between the respective signaller's and recipient's positions (for both body side and visual field) and the emotional context, interactions that require further investigations to understand better their influence on primates' gestural communication with conspecifics.

4) Gesture type

As previously pointed out, the gestural repertoire of non-human primates is rich and varied (e.g. Call & Tomasello 2007). Some researchers have studied whether or not the type of gesture could influence manual laterality. Hobaiter and Byrne (2013) showed that chimpanzees in the wild used their right hands significantly more for non-object-manipulation gestures than for object-manipulation gestures. Hopkins and colleagues (Hopkins & Leavens 1998; Hopkins & Wesley 2002) showed that captive chimpanzees used their right hand more for begging humans than for pointing at them. Moreover, chimpanzees who vocalized during trials were more likely to use their right hand than those that did not vocalize (Hopkins & Leavens 1998; Hopkins & Cantero 2003; Hopkins et al. 2005a). One cannot, however, exclude that this greater right-hand use could be more the consequence of the chimpanzees' emotional state than the emission of a vocalization. To date, only a few types of gestures have been considered but it appears from the literature that right-hand use depends on gesture type. Therefore, to go further, we can wonder whether some gesture characteristics are better markers than others of the right-handedness/left-brain specialization for language. To our knowledge, no study has already investigated the possible effect on manual laterality of the following gesture characteristics: gesture sensory modality (tactile, visual and auditory), the degree of gesture sharing (common gestures performed by most of the subjects in the population vs. rare gestures performed by only a few subjects in the population) and gesture duration (long lasting vs. short lasting). To summarize, many factors appear to modulate manual laterality. Some of them have been partly addressed in gestures and some other never. Therefore, it is essential to go further by considering as much of these factors as possible when investigating manual laterality. In addition, it is also particularly important to care about

methodological issues which can also be source of biases leading to erroneous results and/or interpretation as well as inconsistencies between studies.

3.2.3. Methodological issues

The non-human primate literature on handedness (e.g. Marchant & McGrew 2013) presents several methodological issues as well as inconsistencies between studies that make comparisons difficult such as terminology, measurement method (i.e. spontaneous actions or experimental tasks, non-communication actions or gestures, gestures directed towards humans and/or conspecifics), settings (captivity or wild) as well as procedures related to data recording and analysis (sample size, number of data points per subject, independence of data, factors considered and statistical tests). Another reason of disparities between studies is that they did not use a comprehensive approach taking into account simultaneously multiple influential factors and their interactions. Indeed, as far as we know, no previous study has applied such approach to investigate simultaneously the effect on laterality of the above mentioned individual sociodemographic factors for both signaller and recipient and of characteristics related to the interactional context (visual field and body side of both signaller and recipient and emotional valence of the context) and to the nature of the gesture (e.g. sensory modality, use of communication tool, degree of sharing and duration). Furthermore, no previous study has considered several narrow categories of age (i.e. immature, adolescent, young and mature adult and elder) and hierarchy (i.e. dominant, intermediate and subordinate). Such approach will be used in the present PhD thesis.

3.2.4. Importance of studying laterality in purely intraspecific gestures

Little is still known about laterality of gestures in purely intraspecific communication although studying communication between conspecifics in real-life social context (i.e. closed to contexts in which natural selection has acted) would be necessary to better understand gestural laterality in an evolutionary perspective. Indeed, among research investigating laterality in non-human primates' gestural communication, many studies have considered human-directed gestures (i.e. under experimental conditions) in several species including chimpanzees (e.g. Hopkins & Leavens 1998; Hopkins & Cantero 2003, Meguerditchian et al. 2012), olive baboons (e.g. Meguerditchian & Vauclair 2006; Meunier et al. 2012; Bourjade et al. 2013), Tonkean macaques and tufted capuchins (Meunier et al. 2013c) as well as red-capped mangabeys and Campbell's monkeys (Maille et al. 2013a). By contrast, there are only

few studies having analyzed gestural laterality in purely intraspecific communication (chimpanzees: Fletcher & Weghorst 2005; Meguerditchian et al. 2010a; Hobaiter & Byrne 2013; bonobos: Chapelain 2010; olive baboons: Meguerditchian & Vauclair 2006). Among these studies, only the ones of Meguerditchian and colleagues (2010) and Meguerditchian and Vauclair (2006) evidenced a right-hand preference at the population level, the three other studies overall did not find any population-level bias possibly because they had a low number of subjects and/or insufficient number of data per subject. As far as we know, no study has already investigated laterality in purely intraspecific gestural communication of gorillas. Only Shafer (1987) has addressed gestural laterality of gorillas in communication between conspecifics but she considered a category of undistinguished types of hand motions (a category she called "gestures" but which did not match our definition of gestures) defined as "any hand motions interpreted as signalling to another gorilla or that were interpreted as solitary gestures" p. 51. She collected 663 data points of "gestures" and no information was provided of use of discrete bouts (i.e. sequences of gestures separated by intervals) or frequencies (i.e. every event in a bout) to collect these data points (e.g. Marchant & McGrew 1991; Byrne & Byrne 1991). She found that the majority of individuals which performed at least 6 times "gestures" (i.e. 18 gorillas over the 47 considered from 5 zoos) were non-lateralized but her results revealed that "gestures" presented a trend towards the right side. A particular interest of the present PhD thesis is to focus only on intraspecific gestures.

3.2.5. Importance of comparing manual laterality between non-communication actions and gestures

To investigate whether manual actions performed in manipulations and gestures are controlled by different lateralized cerebral structures in non-human primates, several studies have compared manual laterality in both non-communication actions and gestures (e.g. chimpanzees: Meguerditchian et al. 2010a; red-capped mangabeys and Campbell's monkeys: Maille et al. 2013a). These studies found a greater right-hand use in gestures than in non-communication actions leading the authors to support to the hypothesis that manipulation and communication components would not share the same lateralized cerebral system in certain primates (e.g. Meguerditchian & Vauclair 2009). As far as we know, however, none of these studies has considered purely intraspecific communication in their comparisons. Moreover, no existing study has already compared manual laterality in tool-use manipulations and in gestures involving a tool in order to assess the effect peculiar to communication on laterality.

4. Research questions and predictions

As in humans (e.g. Healey et al. 1986; Steenhuis & Bryden 1989), handedness in non-human primates (e.g. Wesley et al. 2002) appears to be multidimensional. All the above-mentioned findings emphasize the importance of investigating deeper non-human primates' gestural communication in order to better understand the evolutionary origins of human language and to clarify the relationship between language lateralization and handedness. To do so and to overcome discrepancies and fragmented knowledge from previous studies, it is thus important to take into account as many potential influential factors as possible using a comprehensive analysis capable of assessing as much rigorously as possible the distinct influence of each one and their interactions on gestural laterality.

The goal of the present PhD thesis was to take part in the research effort devoted to the understanding of the evolutionary relationship between the right direction of handedness and the left-cerebral lateralization of language in humans. In particular, we wondered (1) whether it is possible to evidence effect of social pressures on intraspecific communication considering multiple factors related to social interactions and (2) whether some gesture characteristics are better markers than others of the right-handedness/left-brain specialization for language. To serve this goal, we implemented a multifactorial investigation to study manual laterality in real-life social-ecological situations of two humans' close living relatives: chimpanzees (*Pan troglodytes spp.*) and Western lowland gorillas *(Gorilla gorilla gorilla).* Both species are very close phylogenetically to humans with a complex social life, a rich gestural communication, and complex tool uses. Moreover, these two species differ in their social structure and dynamics: chimpanzees live in multi-male–multi-female groups characterized by a highly variable party membership whereas gorillas live in polygamous and generally cohesive groups (Aureli et al. 2008). Choosing such species with different social structure and dynamics will enable us to check the possible influence of these social-related factors on intraspecific gestural laterality.

To achieve our goal, we investigated first systematically the production of the most frequent gesture types of their communication repertoire (e.g. chimpanzees: Nishida et al. 1999, 2010; gorillas: Pika et al. 2003; Genty et al. 2009). Second, we compared manual laterality in the context of tool-use in non-communication actions and gestures to assess a possible effect peculiar to the function (non-communication or communication).

In the present PhD thesis manuscript, we successively considered the five following questions and associated hypotheses:

(1) Is there a bias at the population level[11] in intraspecific gestural laterality for chimpanzees and for gorillas?

To answer this question, we analysed each of 21 (resp. 16) intraspecific gestures of chimpanzees (resp. gorillas) separately. According to existing literature on primates' gestural laterality, we predicted that a majority of these frequently expressed gestures would be right-lateralized at the population level.

(2) Which factors influence intraspecific gestural laterality of chimpanzees and of gorillas?

To answer this question, the three following categories of factors were taken into account simultaneously: the interactional context components (visual field and body side of both signaller and recipient and the emotional valence of the context), gesture characteristics (sensory modality, use of communication tool, duration and degree of sharing) and individual sociodemographic characteristics of both signaller and recipient (age, sex, group, hierarchy, kinship and affiliation). According to literature on laterality in social behaviours mentioned above, we expected that signallers' gestural laterality would be particularly modulated by interactional context, gesture characteristics and individual social characteristics.

(3) Does intraspecific gestural laterality of chimpanzees differ from the one of gorillas and if yes which factors could explain this difference?

We expected a possible difference in gestural laterality between both species related to their particular social structure and dynamics.

(4) Does manual laterality of chimpanzees[12] differ at the population level when considering tool use in both non-communication actions and gestures?

To answer this question, we examined each of five frequently expressed conspecific-directed gestures involving the use of a tool also reported in wild chimpanzees (e.g. Nishida et al. 2010) and a non-communication tool use action similar to termite fishing (e.g. in wild chimpanzees: McGrew & Marchant 1992). According to previous findings in chimpanzees for termite fishing (e.g. Bogart et al. 2012) and for gestures (e.g. Hopkins et al. 2012; Meguerditchian et al. 2013), we predicted a marked laterality at the population level (i.e. most

[11] In this study our population includes all our subjects of the same species.

[12] Because of an insufficient amount of data collected for gorillas, the study of the influence of the function (non-communication versus communication) on manual laterality in tool-use actions was limited to the chimpanzees.

individuals being lateralized) towards the left for the considered non-communication tool-use action and towards the right for the gestures involving a tool.

(5) Is manual laterality of chimpanzees in both non-communication actions and gestures modulated by individuals' sociodemographic characteristics (age, sex, hierarchical rank, and group)?

To answer this question, we considered simultaneously the effects of age, sex, hierarchical rank, and group and their possible interactions. Based on literature on chimpanzees (e.g. Hopkins et al. 2009), we expected modulation by age, sex, and hierarchy but not by group.

Currently, findings concerning these five questions are the subject of three articles submitted to peer-reviewed scientific journals. Chapter 3 presents the two articles addressing solely chimpanzees'/gorillas' intraspecific gestural laterality. Chapter 4 presents the third article comparing manual laterality in the context of tool use considering both intraspecific gestures and non-communication actions.

CHAPTER 2

General methodology

1. Presentation of the studied species

1.1. Chimpanzee

In the present study, we followed the 39 chimpanzees housed in three different zoos located in Europe (Leipzig Zoo (Germany), Beauval Zoo and La Palmyre Zoo (France)). According to information provided by the zoos, we studied 15 individuals belonging to the following subspecies of chimpanzee *Pan troglodytes verus* and 4 *P. t. troglodytes*. The others were hybrids: 3 individuals between *P. t. verus and P. t. schweinfurthii,* 1 individual between *P. t. troglodytes and P. t. verus,* and 1 individual between *P. t. troglodytes and P. t. schweinfurthii.* In addition, hybridization was unknown for 15 individuals.

1.1.1. Phylogeny and geographical distribution

Molecular phylogenetic studies have estimated that the genetic split between chimpanzees (*Pan troglodytes)* and humans have occurred approximately 5–7 million years ago (Mya) (Ruvolo et al. 1991; Bailey et al. 1992; Chen & Li 2001; Brunet et al. 2002; Patterson et al. 2006). Until recently, chimpanzees were considered to be our closest living evolutionary relatives according to both catalogs of genomic features of humans (International Human Genome Sequencing Consortium, 2004) and of chimpanzees (The Chimpanzee Sequencing and Analysis Consortium, 2005). However, recent completion of the bonobo genome (Prufer et al. 2012) has revealed that bonobos (*Pan paniscus*) are as close to humans as chimpanzees are: the humans 'ancestor would have split from the common ancestor of chimpanzees and bonobos approximately 4–7 Mya.

More recently, Langergraber and colleagues (2012) have estimated the chimpanzee–human split times at 6.8–11.6 million years based on direct observations of chimpanzee and human generation times and rates of mutation per generation in humans. This is coherent with the study of Venn and colleagues (2014) who have compared mutation rates of humans and chimpanzees and have estimated that human and chimpanzee ancestors' genomes would have begun to diverge (not necessarily split) about 12-13 Mya. Genetic studies of mitochondrial DNA (mtDNA) (Gonder et al. 1997, 2006; Bradley & Vigilant 2002) have distinguished four chimpanzee subspecies which are: western chimpanzees (*Pan troglodytes verus),* Cameroon-Nigeria chimpanzees *(Pan troglodytes elioti* formerly *Pan troglodytes vellerosus),* central chimpanzees *(Pan troglodytes troglodytes),* and eastern chimpanzees *(Pan troglodytes schweinfurthii).* However, the number of species and subspecies of the Genus *Pan* is still

debated. Indeed, Groves (2005) has studied craniometric variation of *P. t. schweinfurthii* and has suggested splitting it into two subspecies *P. t. schweinfurthii* and *P. t. marungensis*. Furthemore, Becquet and colleagues (2007) have analyzed the genetic structure of chimpanzee populations using the largest dataset to date and have indicated that they have not detected the existence of the fourth population/subspecies (*P. t. elioti* formerly *P. t. vellerosus*). Lastly, a new population genetics study (Gonder et al. 2011) have recognized three major genetically distinct populations of chimpanzees: Upper Guinea in western Africa (*P. t. verus*), the Gulf of Guinea region (*P. t. ellioti*) and equatorial Africa (*P. t. troglodytes* and *P. t. schweinfurthii*) (see geographical distribution and phylogeny in Figure 1).

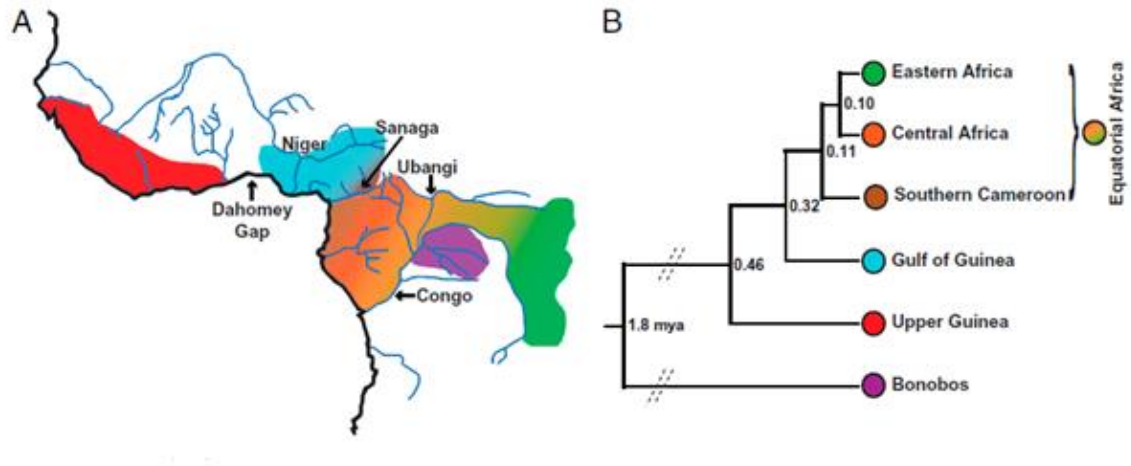


Figure 1 (taken from Gonder and colleagues (2011)): Proposed population structure of Pan, including chimpanzees from the Gulf of Guinea region. (A) Population distribution map. (B) Times to the most recent common genetic ancestor between populations and phylogeny.

1.1.2. Morphology

There is no or weak morphological differentiations between the four chimpanzee subspecies (Albrecht & Miller 1993; Shea et al. 1993; Fisher et al. 2006). Chimpanzees are slightly sexually dimorphic. According to many authors (e.g. Goodall 1986; Jones et al. 1996; Napier & Napier 1985; Nowak 1999; Rowe 1996), adult chimpanzees lengths vary between 635 mm and 925 mm and can be 1 to 1.7 m when standing up. Adult body mass average 50 kg for males and 40 kg for females (Figure 2). Arms and hands are longer than legs and feet, respectively. Chimpanzees have opposable thumbs on hands and feet. During quadrupedal locomotion, chimpanzees knuckle-walk (i.e. they support themselves by means of the second phalange of their fingers) allowing them to carry small object in the fingers. Chimpanzee's coat is usually black or mottled with brown which can turn grey with age for both sexes. They

have no hair on their face, fingers, palms of the hands, and soles of the feet exposing fair skin when they are infants while black skin when they are adults. Infants are also characterized by a white tuft of hair in the anal region. The estrus cycle of females lasts around 36 days. At the peak of estrogen secretion (at about day 15 of the cycle), the anogenital skin swelling of females is particularly remarkable.



Figure 2: A male (left picture) and a female (right picture) adult chimpanzees of the Beauval zoo.

1.1.3. Ecology

Chimpanzees are both terrestrial and arboreal, with time spending on the ground depending both on study sites and sex (Doran 1996). Chimpanzees inhabit a great diversity of habitats from dry woodland savannah, and grassland to tropical rainforest and mountain forest at an altitude of 2750m (e.g. Goodall 1986; Jones et al. 1996; Nowak 1999). Chimpanzees are generally omnivorous and frugivorous even though they can also be herbivorous, insectivorous and carnivorous during some seasons and in some geographic areas (e.g. Goodall 1965, 1968, 1986). Many researchers have documented that chimpanzees make and use tool such as for termite-fishing, wadge-dipping and nuts-cracking. It is interesting to note that there are various tool use patterns observed between communities suggesting the existence of social or cultural learning traditions (e.g. McGrew 1994; Tomasello 1994;

Matzuzawa 2001; Whiten et al. 2001). It has also been reported that chimpanzees hunt large vertebrates such as bush pigs (*Potamochoerus larvatus*) or more generally young colobus monkeys (*Colobinae*). To do this, they use different strategies (depending on populations): some populations chase prey opportunistically whereas others form large cooperative hunting party of males to chase fast-moving prey (e.g. Boesch 1994).

1.1.4. Social structure, organization and behaviours

Chimpanzees in the wild live in multi-male and -female communities composed of 10 to 180 individuals which exhibit a fission-fusion social system (e.g. Goodall 1968, 1986; Nishida 1990; Boesch & Boesch-Achermann 2000; Mitani et al. 2002; Reynolds 2005). Societies characterized by fission-fusion dynamics consist of subgroups of variable size and composition in which group members regularly join (fusion) or separate from (fission) one another (Kummer 1971). This social structure enables individuals to separate temporarily from one another when costs of grouping are high, and to aggregate when costs of grouping are low or benefits of sociality are high (reviewed by Wrangham et al. 1993; Aureli et al. 2008).

Male chimpanzees are strongly philopatric while females generally leave their natal community when they reach sexual maturity (e.g. Boesch & Boesch-Achermann 2000; Mitani et al. 2002). Male chimpanzees are particularly gregarious compared to females (Mitani 2009) even if the latter can also form strong social bonds (Lehmann & Boesch 2009; Langergraber et al. 2009). It has also been shown that males exhibit more diverse affiliative and cooperative behaviours (e.g. party association, grooming, proximity maintenance, coalitions, meat sharing and territorial boundary patrols) (Mitani et al. 2002; Muller & Mitani 2005) than females (Langergraber et al. 2009). According to several studies (e.g. Riss & Goodall 1977; Nishida 1983), formation of strategic short-term coalitions and long-term alliances would be particularly beneficial in terms of fitness. Indeed, such formations would allow establishment and maintenance of dominance hierarchy for both males (Nishida 1983; Nishida & Hosaka 1996) and females (Lehman & Boesch 2007) which would increase reproductive success (for males: e.g. Boesch & Boesch-Achermann 2000; Vigilant et al. 2001; Newton-Fisher et al. 2010; for females: e.g. Pusey et al. 1997; Murray et al. 2006). However, Wroblewski and colleagues (2009) have shown that low-ranking males can also have access to females through female mate choice (Stumpf & Boesch 2005) and alternative male mating strategies such as consortship (when a male–female dyad travels alone and copulates away from other

community members). Dominance hierarchy in males can be linear (Mahale K-group: Nishida 1979; Mahale M-group: Nishida & Hosaka 1996; Kibale Ngogo: Watts 1998; Taï North-group: Boesch & Boesch-Achermann 2000) or in narrow rank classes (Budongo Sonso: Newton-Fisher 2002; Gombe Kasakela: Bygott 1979; Goodall 1986). On the contrary, rank orders would tend to be less marked in females. Indeed, it has been shown that they can be ordered in broad rank classes (Gombe Kasakela: Pusey et al. 1997; Kibale Kanyawara: Wrangham et al. 1992). In some study sites, researchers did not succeed in establishing at least two-thirds of the dyadic dominance relationships within females (Mahale M-group: Nishida 1989; Budongo Sonso: Fawcett 2000). Linearity of the hierarchy in females has been documented only in one study site (Taï National Park: Wittig & Boesch 2003; Lehmann & Boesch 2005).

Chimpanzees are strongly territorial and communities use home ranges of 5 to 35 km^2 (e.g. Boesch & Boesch-Achermann 2000; Goodall 1986; Herbinger et al. 2001; Nishida 1979; Lehmann & Boesch 2003). Conflicts between neighboring chimpanzee communities occur occasionally and can result in lethal coalitionary attacks (Mitani et al. 2010; Wilson & Wrangham 2003). According to Mitani and colleagues (2010), such attacks would lead to territorial expansion. Total community size would not be the best predictor to explain home range size in chimpanzees (Boesch & Boesch-Achermann 2000; Goodall 1986; Lehmann & Boesch 2003). Indeed, home range size would rather be dependent on fruit availability, the number of males and probably other factors such as relative fighting power of males (Lehmann & Boesch 2003; Boesch et al. 2008).

Chimpanzee's communicative behaviours include vocalizations, facial expressions and gestures (e.g. Goodall 1968, 1986; Call & Tomasello 2007). Hobaiter and Byrne (2011a) have recently reported that wild chimpanzees use 66 distinct gesture types to communicate with conspecifics of which 24 gestures shared with gorillas and orangutans.

1.2. Gorilla

We studied the 35 gorillas housed in three different zoos located in Europe: La Vallée des Singes (France), Apenheul and Burgers (The Netherlands). According to information provided by the zoos, all the individuals were western lowland gorillas (*Gorilla gorilla gorilla*).

1.2.1. Phylogeny and geographical distribution

Four gorilla subspecies have been recognized: two western gorilla subspecies (the western lowland gorillas (*Gorilla gorilla gorilla*) and the cross river gorilla (*Gorilla gorilla diehli*)) as well as two eastern gorilla subspecies (the eastern lowland gorillas (*Gorilla beringei graueri*) and the eastern mountain gorillas (*Gorilla beringei beringei*)) (Sarmiento & Oates 2000; Groves 2001; Stumpf et al. 2003; Taylor & Goldsmith 2003; Clifford et al. 2004; Anthony et al. 2007) (see geographical distribution in Figure 3).

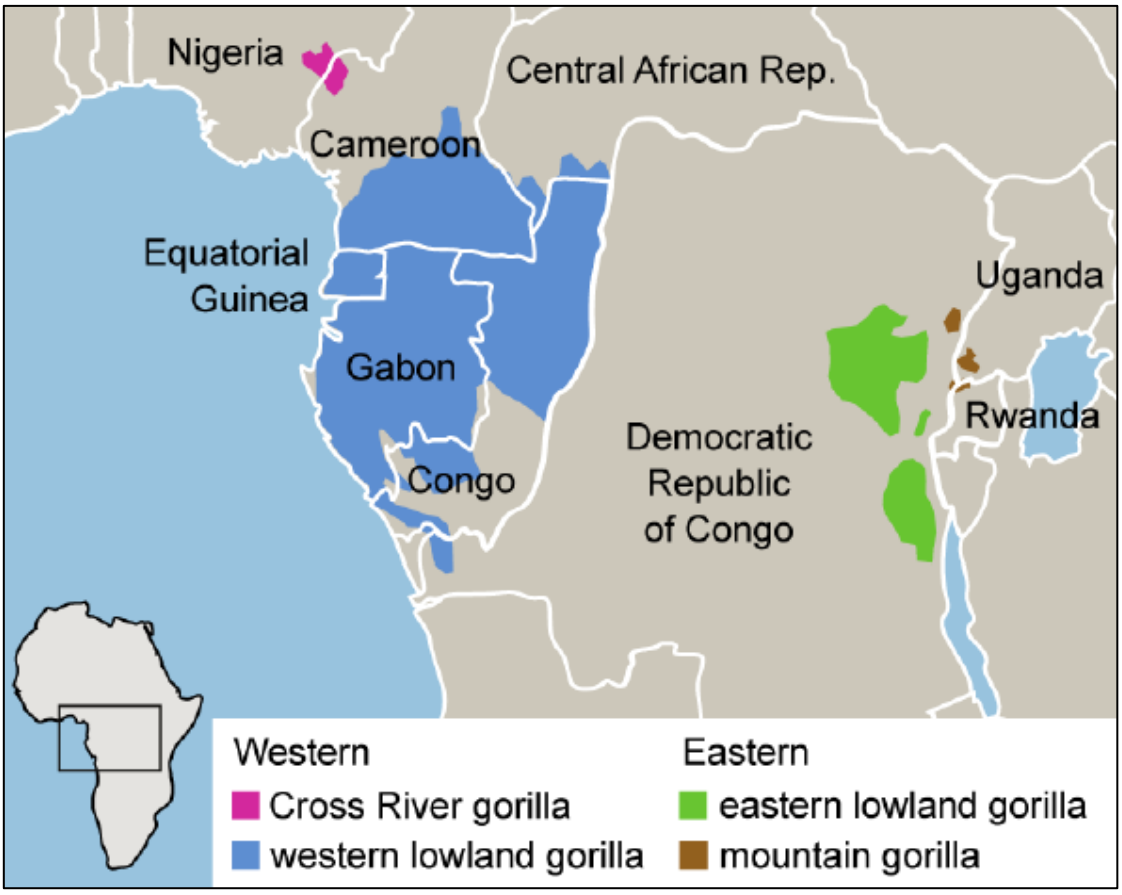


Figure 3 (taken from Scally and colleagues (2012)): Distribution of gorilla subspecies in Africa.

Based on genetic and fossil evidence, Scally and colleagues (2012) have evaluated the split between the gorilla lineage and the lineage leading to humans, chimpanzees, and bonobos at approximately 6 and 10 Mya. Based on gorilla and human generation times and rates of mutation per generation in humans, this split has been estimated at 10.9–17.2 million years (Langergraber et al. 2012).

According to Scally and colleagues (2012), the average genomic sequence divergence between the western and eastern gorilla would have begun about 1.75 Mya. This is coherent with the Thalmann and colleagues' (2007) study which have estimated via simulations of scenarios of population divergence based on nuclear sequences that western and eastern gorillas may have initially diverge around 0.9-1.6 Mya then may have split about 80,000 years ago. Genomic divergence between the two lineages of eastern gorillas would have begun to diverge (not necessarily split) approximately 400,000 years ago (Ruvolo et al. 1994; Garner & Ryder 1996; Jensen- Seaman & Kidd 2001). To our knowledge, no estimation has been performed between the two lineages of western gorillas yet.

1.2.2. Morphology

Gorillas are the largest and one of the most sexually dimorphic primate species: mature adult male gorillas have almost twice more total body mass, 20% greater body length, and larger gluteal muscles than adult females (Plavcan & Van Schaik 1997; Smith & Jungers 1997; Breuer et al. 2007). The western gorillas have smaller and lighter body as well as shorter and narrower chest than eastern gorillas (Rowe 1996; Nowak 1999). They are also characterized by their short brown hair on their heads.

Among the four subspecies of gorillas, *G. gorilla gorilla* is the most sexual size dimorphic one. Indeed, adult body height averages 1.7 m for males and 1.5 m for females (Rowe 1996; Williamson & Butynski 2013) (Figure 4). In the wild, adult body mass averages 140 kg for males and 70 kg for females (Williamson & Butynski 2013). In captivity, mature adult male gorillas, called silverbacks because of the grey fur extending with age from their back to their rump and thighs, can weigh up to 227 kg (Rowe 1996). Arms and hands are longer than legs and feet, respectively. Gorillas have opposable thumbs on hands and feet. Gorillas knuckle-walk during quadrupedal locomotion. Silverbacks have larger head morphology than females because they possess a prominent sagittal crest (i.e. a fibrous adipose tissue) on top of their head and powerful temporal and nuchal muscles connected to a median sagittal bone crest and an occipital bone crest (Straus 1942; Gregory 1950; Dixson 1998). They also have larger canines than females (Plavcan & Van Schaik 1997). Gorillas possess laryngeal sacs (Gregory 1950). They use it as resonance organ during chest beating (Meder 1993).



Figure 4: A silverback surrounded by three adult females and their offspring in the outdoor enclosure of the Burgers' zoo.

1.2.3. Ecology of the study subspecies G. gorilla gorilla

Western lowland gorillas are mainly terrestrial although they are capable to climb into trees especially the youngster (Ankel-Simons 2007). Its habitat is diverse, from primary and secondary lowland rainforest, to large swampy forest clearings where they can feed on mineral-rich herbaceous vegetation (Magliocca & Gautier-Hion 2002). Western lowland gorillas are folivores and opportunistic frugivores (Tutin et al. 1991; Tutin & Fernandez 1993; Bermejo 2004). During dry season when ripe fruits are scarce, they mainly consume vegetative plant parts such as leaves, woody pith, stems and bark and foraging effort (estimated by daily path length) tend to increase (Goldsmith 1999; Tutin 1996).

1.2.4. Social structure, organization and behaviour of G. gorilla gorilla

The social structure and organization of Western lowland gorillas are much less documented compared to the ones of chimpanzees. To our knowledge, western lowland gorillas maintain year-round associations in groups of usually 5 to 10 individuals but some groups can number as 20 to 32 individuals (Bermejo 2004; Williamson & Butynski 2013). Western lowland gorillas live in polygamous harem groups controlled by a silverback male (e.g. Gatti et al. 2004) and generally characterized as cohesive (Aureli et al. 2008). A group is commonly constituted by one silverback, 3 to 4 adult females, and their immature offspring (Parnell 2002b; Gatti et al. 2004; Breuer et al. 2010). Groups composed of more than one mature adult male are rare (e.g. Parnell 2002a; Tutin 1996). Indeed, subordinate males

generally leave their natal community before reaching full sexual maturity to become solitary (Parnell 2002b; Stokes et al. 2003; Robbins et al. 2004). When becoming silverbacks, 80% of them may ultimately acquire females and form their own harem (Parnell 2002b; Gatti et al. 2004; Breuer et al. 2010). Social system of western gorilla is thus characterized by male dispersal but also by female transfer which would prefer smaller groups (Stokes et al. 2003; Tutin 1996). Such reproductive strategies would explain why multimale groups have been rarely observed (Parnell 2002a; Tutin 1996).

Gorillas are not territorial and neighboring groups regularly overlap home ranges of 5 to 30 km^2 (e.g. Bermejo 2004; Cipolletta 2003). Home range size of a group would be dependent on fruit availability and on female transfers between groups (e.g. Bermejo 2004; Cipolletta 2003). Conflicts between neighboring silverbacks are commonly restricted to threat displays (e.g. chest beating) and infrequently result to fatal fights (e.g. Sicotte 1993; Robbins 2003; Caillaud et al. 2008). Comparatively to chimpanzees (e.g. Wilson & Wrangham 2003; Mitani et al. 2010), such non-aggressive intergroup interactions in western lowland gorillas could be explained by kin-biased selection. Indeed, it has been shown that silverbacks are generally genetically related to one or more neighboring ones (Bradley et al. 2004).

As the well-known mountain gorillas (e.g. Fossey 1972; Harcourt et al. 1993), western lowland gorillas's communicative behaviours include vocalizations, facial expressions and gestures (e.g. Fay 1989; Waller & Cherry 2012; Salmi et al. 2013). Concerning gestures, Genty and colleagues (2009) have reported that western lowland gorillas use 102 different gestures. Pika and colleagues (2003) focusing on young individuals (1 to 6-year-old) have reported 33 different gestures.

2. Presentation of the study sites and subjects

2.1. Study sites

The greater the ecological validity of the study, the better (e.g. Marchant & McGrew 2013). Good captive conditions were thus required to ensure subjects to express behaviour as natural as possible. Behavioral observations took place in 6 European zoos: three zoos for chimpanzees (Leipzig Zoo (Germany), Beauval Zoo and La Palmyre Zoo (France)) and three other zoos for gorillas (La Vallée des Singes (France), Apenheul Primate Park and Burgers' Zoo (The Netherlands)) (see geographical location in Figure 5).



Figure 5: Geographical location of the study sites.

These zoos were chosen because they provide relatively similar living conditions to the studied chimpanzees and gorillas (i.e. large naturalistic enclosures and social groups composed of many individuals). The zoo enclosures and their arrangements varied, however, all outdoor enclosures offer semi-natural environment surrounded by a water ditch and contained climbing structures (e.g. trees, ropes and platforms) as well as vegetation (e.g. bamboos and various types of bushes and grass) (see for example Figure 6). All indoor enclosures also included climbing structures (see for example Figure 6). The ones in the zoos of Leipzig and La Palmyre also contained vegetation such as bushes and grass. In addition to climbing structures and vegetation, additional enrichments were proposed to chimpanzees in the three zoos: the 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. Branches were also proposed as additional enrichments to gorillas. The latter have thus much less opportunity to use sticks as a tool compared to chimpanzees.



Figure 6: Indoor (left picture) and outdoor (right picture) enclosures of the Leipzig zoo.

Zookeepers fed the studied subjects three to five times a day (depending of the zoos) with diverse types of fresh fruits, vegetables, branches with leaves, seeds, wood, and raisins supplemented by primate pellets, vitamins and mineral drinks. Water was available *ad libitum*.

2.2. Study subjects

2.2.1. Chimpanzees

In total, 39 chimpanzees were considered including 13 males and 26 females with their ages ranging from 0.7 to 54 years (M = 20.9, SD = 2.14) (see below Table 1). Following Goodall (1986) age categories of the subjects were defined as follows: immatures (0–7 years old), adolescents (8–12 years old), young adults (13–20 years old), mature adults (21–35 years old), and elderly (over 35 years old). The majority of the chimpanzees were mother-reared. Here is the distribution of the studied chimpanzees with respect to the three zoos considered.

Leipzig Zoo, Germany: Chimpanzees are housed in social group composed of 16 individuals (see Table 1) in indoor (430 m^2) and semi-natural outdoor enclosures (4125 m^2).

ZooParc de Beauval), France: Chimpanzees are housed in a social group composed of 14 individuals (see Table 1) in indoor and semi-natural outdoor enclosures of approximately 200 m^2 and 2000 m^2 respectively.

Zoo de La Palmyre, France: Chimpanzees are housed in a social group composed of 9 individuals (see Table 1) in indoor and semi-natural outdoor enclosures of 306 m^2 and 960 m^2 respectively.

Table 1: Names, age, age category, sex and location of each studied chimpanzee.

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

2.2.2. Gorillas

In total, 35 gorillas were considered including 12 males and 23 females with their ages ranging from 0.5 to 42 years (M = 13.6, SD = 2.21) (see Table 2). Age categories of subjects were mainly based on Breuer and colleagues (2009) for infants (0-3 years), juveniles (4–6 years) and adolescents (7-11 years) and on Stoinski and colleagues (2013) for young adults (12-20 years) and mature adults (>20 years) (Table 2). The majority of the gorillas were mother-reared. Here is the distribution of the studied gorillas with respect to the three zoos considered.

La Vallée des Singes, France: Gorillas are housed in a social group composed of 11 individuals (see Table 2) in indoor and semi-natural outdoor enclosures of approximately 125 m^2 and 3800 m^2 respectively.

Apenheul Zoo, The Netherlands: Gorillas are housed in a social group composed of 14 individuals (see Table 2) in indoor and semi-natural outdoor enclosures of approximately 330 m^2 and 10000 m^2 respectively.

Burgers' Zoo, The Netherlands: Gorillas are housed in a social group composed of 11 individuals (of which one newborn gorilla not included in the study) (see Table 2) in indoor and semi-natural outdoor enclosures of approximately 225 m^2 and 3200 m^2 respectively.

Table 2: Name, age, age category, sex and location of each studied gorilla.

Name	Age	Sex	Zoo
Mature adult (over 20 years)			
Virunga	42	F	Vallée des Singes
Gaja	40	F	Vallée des Singes
Lobo	39	F	Apenheul
Mintha	38	F	Apenheul
Mandji	37	F	Apenheul
Yaoundé	28	M	Vallée des Singes
Moséka	28	F	Vallée des Singes
Bauwi	24	M	Burgers' zoo
Young adult (12–20 years)			
N'Gayla	20	F	Burgers' zoo
Makoua	19	F	Burgers' zoo
Jambo	18	M	Apenheul
Shatilla	16	F	Burgers' zoo
Kisiwa	15	F	Apenheul
Nimba	14	F	Burgers' zoo
Likale	12	M	Burgers' zoo
Adolescent (7–11 years)			
Nemsi	11	F	Apenheul
Gyasi	10	F	Apenheul
N'Aika	8	F	Burgers' zoo
Shailâ	7	F	Burgers' zoo
Sango	7	M	Vallée des Singes
Lomako	7	M	Vallée des Singes
Juvenile (4–6 years)			
Miliki	6	F	Vallée des Singes
N'Akouh	4	M	Burgers' zoo
N'Washi	4	F	Burgers' zoo
Wimbe	4	M	Apenheul
Mapasa	4	M	Apenheul
Touni	4	F	Vallée des Singes
Infant (0–3 years)			
Mfungaji	3	F	Apenheul
Djomo	3	M	Vallée des Singes
Mzungu	1	M	Apenheul
Chama	1	F	Apenheul
Tayari	1	F	Apenheul
Iriki	1	F	Apenheul
Wéfa	0.9	F	Vallée des Singes
Mawété	0.5	M	Vallée des Singes

3. Data collection

3.1. Pilot study

Preliminary observations were performed on the gorillas of La Vallée des Singes (France) during a pilot study between the 1st and the 17th of May 2012. This pilot study allowed me to test the methods in order to select and to practice the most suitable observational procedure to collect, code and analyze data.

During this pilot study, I used two formal observational sampling methods in behavioural research, namely a *focal animal sampling* (Altmann 1974) to be sure to equally observe all the individuals of the studied group, and simultaneously a *sampling all occurrences of some behaviours* (Altmann 1974) to record also the behaviours of interest expressed by the individuals who were closed to the focal individual. However, focusing only on one individual and its spatially closed congeners did not appear to be the most appropriate observational procedure to optimize data collection. Indeed, I encountered some difficulties to observe rather solitary individuals who used to be hidden from view (e.g. individuals staying behind bushes) while at the same time the rest of the group (which was prominent) could have potentially performed gestures of interest (of which some of them are infrequent events). For these reasons, I abandoned *focal animal sampling* and I only used *sampling all occurrences of some behaviours* to maximize data recording. Indeed, I needed to have as much data as possible for each of the considered behaviours in order to carry out reliable individual- and group-level analysis as well as to study the effects of possible influential factors on intraspecific gestural laterality. Importantly, I kept track of recorded behaviours per individual daily to observe each individual the most equally possible.

Data collection was first made by video recording but this procedure did not appear to be the most suitable one. As a matter of fact, because of the large size of the enclosures, the field camera did not permit to fully cover the observation area which is essential when using *sampling all occurrences of some behaviours*. Furthermore, zoom capacity and image quality did not allow accurate identification of individuals when they were far from the border of the enclosure. By contrast, the zoom capacity of binoculars allowed me to do so. When individuals were far away, I could also using binoculars 1) to check that signallers communicating by gestures were not simultaneously holding an object (which would have potentially produced laterality biases for the non-object manipulation gestures considered) and 2) to distinguish types of gestural signalling relatively similar in their form at a distance

(because of perspective effects) but different in their meaning such as TOUCH BODY, ATTEMPT TO REACH, PUNCH, PUSH and SLAP.

3.2. Observation periods

Observations were mainly performed when the weather was good enough in order to collect behavioral data when subjects are in their semi-natural outdoor enclosure.

3.2.1. Chimpanzees

Observational data were collected at the WKPRC at the Leipzig Zoo between the 1st of July and the 20th of September 2013, at Zooparc de Beauval between the 29th of September and the 10th of November 2013 and at La Palmyre between the 23th of November and the 22th of December 2013. This yielded respectively 333 h, 198 h and 174 h observation, for a total of 705 h. It has to be mentioned that the chimpanzees of Leipzig were kept in their indoor enclosure in the morning. Furthermore, the chimpanzees of La Palmyre could only be observed in their indoor enclosure because of low outdoor temperature. Indeed, because of time schedule constraint, observations of the third group of chimpanzees at La Palmyre were performed from the middle to the end of Autumn.

3.2.2. Gorillas

Observational data were collected at La Vallée des Singes between the18th of May and the 25th of July 2012, at Apenheul Zoo between the 14th of August and the 27th of October 2012 and at Burgers' Zoo between the 29th of April and the 29th of June 2013. This yielded respectively 196.5 h, 214.5 h and 240 h observation, for a total of 651 h.

3.3. Observational and coding procedures

3.3.1. Observation procedure

Observations took place from July to December 2013 for chimpanzees and from May 2012 to June 2013 for gorillas, 6 h a day during 4 sessions of 1.5h, two in the morning and two in the afternoon. The sampling rule was *sampling all occurrences of some behaviours* (Altmann 1974) to optimize data recording, particularly not to miss infrequent behaviours such as EMBRACE HALF or THROW. Observation data were collected in real time by using a

stopwatch, a powerful pair of binoculars, and were recorded on a paper sheet. Data were collected in real time by using a stopwatch, a powerful pair of binoculars, and a paper sheet onto which observation data were recorded. Data collection was mostly performed from above and as close as possible to the subjects to allow a clear view of them.

3.3.2. Coding procedure for conspecific-directed gestures

For both species, only dyadic interactions were taken into account. We defined the individual that started the social interaction as the signaller and the target of this interaction as the recipient. For each dyadic interaction, we recorded:

(1) the type of gesture (based on Nishida and colleagues' ethograms, 1999, 2010) and the left or right limb (hand or foot) used by the signaller to communicate,
(2) the interactional context of gestural production considering the relative positions of the two subjects before and during an interaction (both visual field and body side) as well as the emotional context associated with the interaction, and
(3) the identity and role (signaller or recipient) of both subjects, as described below.

Following Pika's definition of gesture (Pika 2008a, 2008b), we considered only intentionally produced gestures that:

(1) were used to initiate (not continue) a social interaction,
(2) were mechanically ineffective (a gesture that "visibly lacks the mechanical force to bring about the reaction shown by the recipient, and also does not include any attempt to grab or extensively hold a body part of the other": Pollick & de Waal 2007, p. 8185), and
(3) included gazing at the recipient, gaze alternation, and/or waiting for a response (e.g. Bruner 1981; Tomasello et al. 1989).

Because only two gestures involved the foot (SLAP FOOT and KICK), we used the term "hand" instead of "limb" for simplicity.

3.3.3. Gesture characteristics

Our gesture classification for both chimpanzees and gorillas was based on previous gestural repertoires (when necessary anatomical elements or precisions were added) (Table 3).

21 different gestures were considered for chimpanzees and 16 different ones for gorillas. These gestures were:

- divided into three communication modalities: visual gestures that generate a mainly visual component with no physical contact, auditory gestures that generate sound while being performed, and tactile gestures that include a physical contact with the recipient (following Pika et al. 2003, 2005) (Tables 4 and 5). These categories respectively correspond to the ones called visible/silent, visible/audible and tactile in Genty and colleagues (2009), Call and Tomasello (2007), and Tanner and Byrne (1996).
- performed either with an object used as a communication tool or not.

We also measured the time subjects took to perform a single gesture: the starting point was determined by a hand starting to move, the end point when the hand was again in a resting position (Kendon 1980; McNeill 1992). Gestures lasting less than 2 seconds were categorized as "short" gestures and gestures lasting more than 2 seconds were categorized as "long" gestures.

The evidence of the effect of social pressures on human laterality (e.g. see reviews Llaurens et al. 2009; Schaasfma et al. 2009) led us to divide gestures into two categories according to their degree of sharing among group members as follows: some gestures were categorized as "rare", defined as gestures performed by only a few subjects in our population (i.e. performed by 13 of the 39 chimpanzees; and by 17 of the 35 gorillas); and the other gestures were categorized as "common", namely defined as gestures performed by most of the subjects in the population (i.e. performed by at least 25 chimpanzees; and by at least 19 gorillas). Such categorization was defined based on the observed gaps in the distribution of the number of subjects (having performed at least six times each a given gesture) between the rare and common gestures for chimpanzees (gap between 13 and 25 individuals) and for gorillas (gap between 17 and 19 individuals) (see gaps in Figure 7). Within the comparative approach of gestural laterality between both chimpanzees and gorillas, it is interesting to note that 13 of the 14 gestures shared by both species are classified in the same categories (rare or common gestures).

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

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

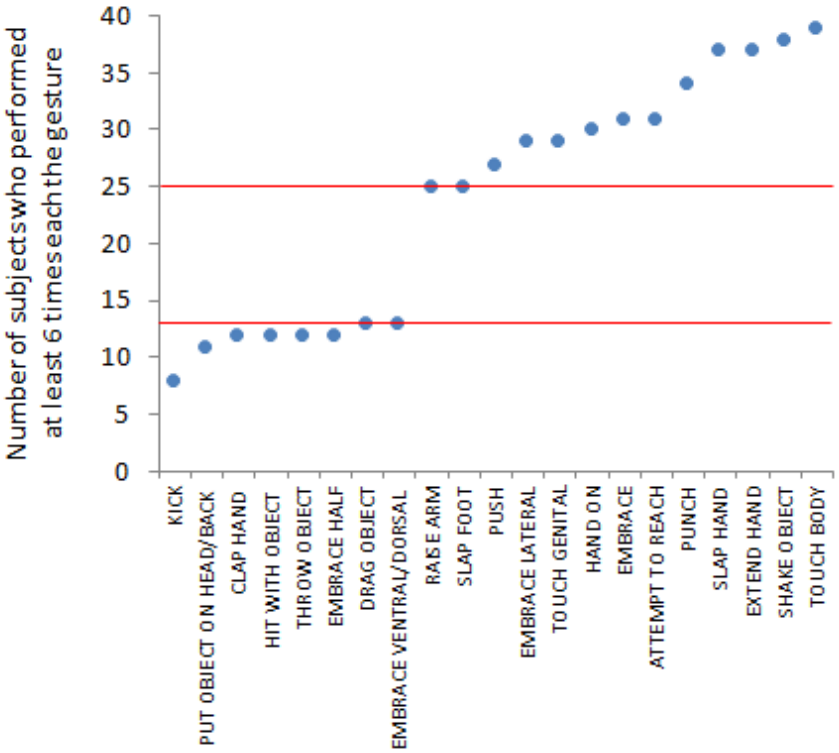
Table 4. Number of gestures per category for each species

Category	Auditory	Tactile	Visual	With object	Without object	Short	Long	Rare	Common
Chimpanzees	3	11	7	5	16	12	9	8	13
Gorillas	4	6	6	4	12	10	6	8	8

Table 5. Gestures are regrouped by sensory modality. (c) refers to chimpanzees only; (g) refers to gorillas only. Object manipulation refers to gestures involving the use of an object ("Yes") or not ("No"). Duration refers to gestures lasting less than 2 seconds ("Short") or more than 2 seconds ("Long"). Sharing degree refers to rare gestures performed by only a few subjects in the population ("Low") or to common gestures performed by most of the subjects in the population ("High").

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

(a)



(b)

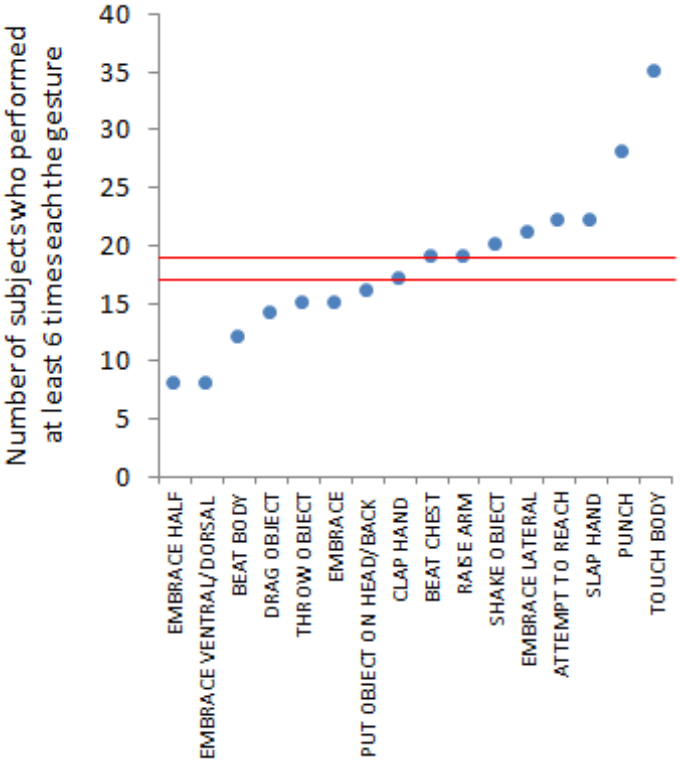


Figure 7: Distribution of the number of subjects (having performed at least six times each a given gesture) between the rare and common gestures for (a) chimpanzees and (b) gorillas. Gap separating rare and common gestures delimited by red lines.

3.3.4. Characteristics of the interactional context of gestures production

For each dyadic interaction, we recorded the relative positions – visual field used and exposed body side – of both subjects before (the last position for 2 seconds before an interaction) and during the interaction. Most interactions were predictable as signallers emitted intentional signals (e.g. gazing at the recipient, gaze alternation, movement towards the recipient).

The emotional contexts of interactions were divided into two categories – positive and negative – according to three criteria. The emotional context was primarily based on the response of the recipient, but also on the associated global social context and on the signallers' expressions if necessary. The emotional context was inferred according to:

(1) the functional consequences of the gesture during an interaction (the response of the recipient to the signaller's gesture). The possible responses of the recipient were: apparent change of the recipient's behaviour including communication responses (via gestural, vocal, facial and/or whole-body expressions) or actions (modification of activity – change or stop –, modification in possession of a resource), or no apparent change in the recipient's behaviour,

(2) the global social context in which the given interaction occurred: aggression, post-conflict reconciliation (contact between former opponents) and consolation (contact of the aggressed party with a third animal), access to food, object or infant, nursing, grooming, mating, play and travel, and

(3) the signaller's facial (Parr & Waller 2006; Parr et al. 2005) and vocal expressions (Crockford & Boesch 2005) and, to a lesser extent, whole-body expressions (e.g. rhythmic movements: Goodall 1989; pilo-erection: Van Hooff 1973; Goodall 1989).

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

Non-communication tool-use actions were observed and recorded during spontaneous daily activities of both chimpanzees and gorillas. We focused on the use of a stick to obtain an out-of-reach goal. This tool manipulation requires precision similarly to termite fishing (e.g. McGrew & Marchant 1992). Because of an insufficient amount of data collected for gorillas, the study of the influence particular to the function (non-communication versus communication) on manual laterality in tool-use actions was limited to the chimpanzees.

In the zoos of Leipzig, Beauval and La Palmyre, the 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 where 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 beyond its edge). For each tool manipulation, we recorded the hand (left or right) used by the subject to obtain the out-of-reach food.

Not all the chimpanzees expressed these behaviours: 25 (of which 6 immatures, 6 adolescents, 4 young adults, 5 mature adults and 4 elders; 9 males and 16 females) of the 39 studied chimpanzees performed enough non-communication tool-use actions to be considered in the study comparing laterality in the context of tool-use in gestures and non-communication actions (Article 2).

3.3.6. Data requirements and independency

Whether for conspecific gestures or non-communication tool use actions, a requirement for any hand to be recorded was that both hands of the subject were free and symmetrically positioned with respect to its body midline before the action (communicative or non-communicative), without any environmental factors which could potentially influence the use of one hand (e.g. being close to a wall/bush/tree) (e.g. Forrester et al. 2013). Data were recorded when an action was produced either singly or in a bout (i.e. sequence of actions separated by intervals) (e.g. Marchant & McGrew 1991; Byrne & Byrne 1991). In the case of a bout, only the first manual action of the sequence was recorded. One of the following criteria must be met to consider that a single action or a bout of actions was terminated:

(1) the subject's hand returned to its initial position (Meguerditchian et al. 2010a),

(2) the subject's hand switched to another non-communicative activity (e.g. forage),

(3) an incident (e.g. stumble) occurred that might influence the use of one of the hands (Hopkins & de Waal 1995; Hopkins et al. 2001b; McGrew & Marchant 2001; Harisson & Nystrom 2010).

To ensure statistical independence of the data, a change in hand activity must last more than 3 seconds before another action can be taken into account (Morris et al. 1993; Hopkins & de Waal 1995).

3.3.7. Sociodemographic characteristics of the subjects

In addition to signaller and recipient's demographic characteristics (age, sex, zoo), we considered for both species data concerning kin and social relationships (affiliation and hierarchy).

3.3.7.1. Kinship

Kinship was determined by genetic analyses and data were provided by each zoo. Three categories of chimpanzee pairs were considered: (1) "Parent-infant" including mother-infant and father-infant pairs, (2) "Siblings" including siblings and half-siblings, and (3) "Unrelated" for pairs of genetically unrelated subjects.

3.3.7.2. Affiliation

To evaluate the general tenor of a relationship, one way is to consider the relative frequencies of affiliative[13] and agonistic[14] behaviours within the dyad (e.g. review Silk et al. 2013a). Two indexes of interest have already been used to evaluate such relationship quality.

Weaver and de Waal (2002) measured relationship quality considering the ratio of the relative rate of affiliative to aggressive interactions. However, this index has two disadvantages:

- it is a ratio so that it is not defined if the denominator (i.e. rate of aggressive interactions) equals zero. In other words, it is impossible to evaluate the relationship quality in dyads engaged in affiliation but not in conflict. Such case was encountered many times considering all the dyads we had (494 dyads for chimpanzees and 422

[13] "Nonagonistic body contact, or invitation for body contact by staring, approaching, and/or gesturing to another; greeting behaviors such as between individuals who were not previously in contact and can include pant grunt, embrace, head bob, and/or gentle touch": Pollick & de Waal 2007, p. 8186.

[14] "Individual performs or receives aggressive behaviors such as bark, grunt, chase, hit/punch, bite, flee, or scream; situations where no clear agonistic behaviors are present but there is clear conflict; reconciliation and support behaviors such as two individuals engaging in friendly body contact while at least one of them seems distressed, frightened, or hurt can be between either aggressor and victim, or between victim and third individual, as well as individual supporting another who is involved in agonism with opponent": Pollick & de Waal 2007, p. 8186.

dyads for gorillas) within the three groups of chimpanzees and three groups of gorillas.

- it gives too much weight to frequently expressed gestures compared to less frequently expressed gestures which are equally informative if not more than the former so, yielding biases

Silk and colleagues' (2006, 2013b) studies of baboons and chimpanzees considered a composite index of sociality (CSI) for each dyad: first, by dividing for each of the considered behaviours (for baboons: grooming and proximity; for chimpanzees: grooming, contact, and proximity), the number of focal samples of the behaviour *i* for a given dyad by the mean number of focal samples that included the behaviour *i* across all dyads; second by averaging over the considered behaviours. However, this CSI has the important disadvantage of not taking into account agonistic behaviours, an essential requirement when assessing affiliation.

To remedy the disadvantages of the above-mentioned indexes and to better evaluate relationship quality within pairs of individuals, we created a Dyadic Affiliation Index (DAI) based on the relative frequencies of affiliative and agonistic behaviours within the dyad. This index increases with affinity, starting from 0 in absence of affinity. It is calculated as:

$$DAI_{xy} = \frac{\left(\frac{\sum_{i=1}^{n} \frac{f_{ixy}}{\bar{f}_i}}{n}\right)}{1 + \left(\frac{\sum_{j=1}^{n'} \frac{h_{jxy}}{\bar{h}_j}}{n'}\right)}$$

Where f_{ixy} is the total number of occurrences of the affiliative behaviour (*i*) expressed by *x* towards *y*; $\bar{f}_i$ is the mean number of occurrencesof the affiliative behaviour (*i*) across all dyads; *n* is the number of affiliative behaviours expressed by *x* towards *y*; h_{jxy} is the total number of occurrences of the agonistic behaviour (*j*) expressed by *x* towards *y*; $\bar{h}_j$ is the mean number of occurrences of the agonistic behaviour (*j*) across all dyads; *n'* is the number of agonistic behaviours expressed by *x* towards *y*. Three categories of dyadic affiliation were considered: (1) "Low" from 0 to 0.5 (389 dyads for chimpanzees and 335 for gorillas), (2) "Medium" from 0.5 to 1 (58 dyads for chimpanzees and 31 for gorillas), and (3) "High" more than 1 (47 dyads for chimpanzees and 36 for gorillas).

Affiliative and agonistic behaviours were selected according to the definitions of Pollick and de Waal (2007). The following strict affiliative gestures (i.e. gestures that are expressed only

in positive contexts) were considered: EMBRACE, EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, EXTEND HAND (only for chimpanzees), and TOUCH BODY. We analysed all these strict affiliative interactions we recorded (8986 for chimpanzees and 4477 for gorillas). We also analyzed all agonistic interactions that occurred (4334 for chimpanzees and 1039 for gorillas). These interactions include the mechanically ineffective gestures considered in the chimpanzee (resp. gorilla) study but also SLAP BODY and SLAP (resp. KICK and SLAP) (Pika et al. 2003) that we did not retain because data concerning these actions did not meet the statistical criteria required for the binomial test (see details below in Descriptive statistics) and two mechanically effective gestures for both chimpanzee and gorilla study: GRAB and PUSH (mechanical effective version) (Pika et al. 2005a).

3.3.7.3. Hierarchy

Following Langbein and Puppe (2004), hierarchical dominance relationships were determined on the basis of agonistic interactions (Pollick & de Waal 2007). Only interactions within dyads for which the aggressor and the receiver of the threat were clearly identified were taken into account.

All recorded agonistic interactions (4334 for chimpanzees and 1039 for gorillas) were taken into account. We organized these interactions into sociometric matrices from which we calculated Kendall's coefficient of linearity *K*, Landau's linearity index *h* and the index of linearity *h'* (de Vries 1995), using MatMan 1.1 (Noldus Information Technology, Wageningen, Netherlands). The index *h'* is based on *h* and takes into account the existence of unknown relationships (when two subjects of a dyad had not been observed to interact aggressively with each other or when they had an equal number of wins and losses). Each index varies from 0 (absence of linearity) to 1 (complete linearity). Statistical significance of *K* was provided by a chi-square test. A resampling process using 10 000 randomizations was performed for the *h'* index (de Vries 1995). When the dominance hierarchy was significantly linear, subjects were reordered by a two-step iterative procedure, finding the rank order most consistent with a linear hierarchy by minimizing the number of inconsistencies and then minimizing the total strength of the inconsistencies (de Vries 1998; de Vries et al. 2006). MatMan 1.1 assigns a rank from 1 (the most dominant) to N (the most subordinate) to each of the N subjects of one zoo. MatMan did not find a linear hierarchy for La Vallée gorillas. The hierarchy of La Vallée gorillas was thus based on the gorillas' zoo keepers' reports. Three

categories of hierarchical rank were considered: "Subordinate", "Intermediate", and "Dominant":

- for chimpanzees: the Beauval group included 5 subordinates, 5 intermediates and 4 dominants; Leipzig group: 5 subordinates, 5 intermediates and 6 dominants; and Palmyre group: 3 subordinates, 3 intermediates and 3 dominants
- for gorillas: Apenheul group: 7 subordinates, 3 intermediates and 4 dominants; Burgers' group: 4 subordinates, 4 intermediates and 2 dominants; La Vallée group: 6 subordinates, 2 intermediates and 3 dominants).

3.4. Data analysis and statistics

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.

3.4.1. Descriptive statistics

To enable subsequent statistical analyses using binominal test (Siegel & Castellan 1988), we only used those behaviours (the considered conspecific-directed gestures and the non-communication tool-use actions) which had been performed at least six times each by a minimum of six subjects (Chapelain 2010).

Binomial tests on the numbers of responses involving the left and right hands assessed individual-level biases for each behaviour. For each subject, the direction of asymmetry was evaluated by calculating an individual Handedness Index (HI) for each subject applying the formula HI= (R-L)/(R+L), where R and L represent the total number of right- and left-hand responses respectively. HI varies from -1.0 to +1.0. Its sign indicates direction of hand preference, positive values correspond to a right-hand preference and negative values to a left-hand preference. The strength of individual hand preference was estimated by the absolute value of HI (ABSHI) varying from 0 to 1. This procedure is similar to that used by previous authors (e.g. Harris & Carlson 1993; Hopkins 1995).

Binomial tests assessed population-level[15] biases in the number of lateralized and non-lateralized subjects for each behaviour. When at least six subjects were lateralized, binomial tests assessed population-level biases in the number of right-handers and left-handers for each behaviour. For each behaviour, we evaluated the bias in hand use at the population level by a

[15] Following previous studies (e.g. Hopkins et al. 2005b), "population-level" refers here for each species to all the individuals of the 3 groups/zoos studied.

one-sample two-sided Student's t-test on the HI values of all the subjects only when the HI distribution was normal (Shapiro-Wilk normality test) and by a one-sample Wilcoxon signed rank test when the HI distribution was not normal.

Spearman correlation tests estimated potential effects of the number of data points per subject on the direction and strength of laterality. Pearson correlation tests checked possible correlations between the visual field and body side of both signaller and recipient as well as before and during an interaction.

3.4.2. Generalized Linear Mixed Model (GLMM) analysis of multiple influential factors

Generalized linear models (GLMs) extend the linear regression approach to different types of dependent variables. In particular, they include logistic regression which corresponds to binary dependent variables as it is the case in our study (hand used: right or left). Fixed variables are those for which we analyze the effect on the dependent variable. Early uses of logistic regression were biomedical applications but it has become popular in business, genetics and ecology applications. This way of analyzing the influence of different factors on dependent variables is very new in primate studies (e.g. Gomes et al. 2009; Romero et al. 2011; Bourjade et al. 2014; Duboscq et al. 2014). It has only recently been applied to examine laterality in primates (Meunier et al. 2013b; Maille et al. 2013b, 2013c) whereas previous studies used nonparametric statistics (e.g. Kruskal-Wallis test, Mann-Whitney test).

The interest of this new type of analysis compared to nonparametric statistics is the following:

- Previous nonparametric statistics methods needed to be implemented separately for each potentially influencing variable which can lead to erroneous conclusions. For instance, a variable can be found ineffective while its effect is masked by the hidden effect of other variables or a variable can be found effective while its effect is in fact produced by another variable.
- Only GLMs allow taking simultaneously into account different potentially influencing variables and their interactions. An interaction between two fixed variables is considered significant if the effect of one of these variables on the dependent variable (e.g. hand used) differs according to the modality of the other variable. GLMs make possible to assess at best the effect particular to a given variable without being affected by the variation due to other variables.

As we have repeated observations on each individual (signaller or recipient) we used an extension of the GLMs named generalized linear mixed model (GLMM). GLMM permits to include signaller and recipient as random variables thus allowing remedying the problem of pseudo-replication (Waller et al. 2013).

For the GLMM analysis, we used the ‘glmer’ function [‘lme4’ package (Bates et al. 2014)] and we selected (iterative procedure) 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 ‘Anova’ function [‘car’ package (Fox & Weisberg 2011]. Least Square means (LSmeans) and associated adjusted probabilities of right-hand use were computed using ‘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 calculated between LSmeans (‘lsmeans’ package).

3.4.2.1. GLMM: study of intraspecific gestural laterality in chimpanzees and gorillas

We evaluated the possible effect of multiple variables on gestural laterality of each species using a logistic regression with hand use as the dependent variable. This GLMM analysis allowed estimation of the effects of interactional context as well as gesture and individual sociodemographic characteristics on hand use.

The fixed variables were: position (Left or Right) of the recipient in the signaller’s visual field during the interaction (noted SVF), position of the signaller in the recipient’s visual field during the interaction (noted RVF), emotional context, gesture characteristics (sensory modality: auditory, tactile or visual; use of communication tool: with or without object, sharing degree: common or rare; duration: short or long) as well as sociodemographic (age, sex, zoo, kinship, hierarchy, dyadic affiliation) characteristics. We included all possible interactions between fixed variables at the beginning of the iterative model selection.

To avoid pseudoreplication caused by repeated observations, we considered signaller’s and recipient’s identities as random variables.

3.4.2.2. GLMM: study of manual laterality of chimpanzees in the context of tool-use in gestures and non-communication actions

To assess differences in hand use between tool-use activities in gestures and in non-communication actions, we used a logistic regression with hand use as the dependent variable. To avoid numerical instabilities in the GLMM procedure, the 5 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 between 4 visual gestures and 1 tactile was justified by the results of Article 1 who did not put in evidence that sensory modality modulated laterality of gestures involving the use of a communication tool. The fixed variables were thus individuals' sociodemographic characteristics (age, sex, hierarchy, and zoo) and "Tool use activity" (two modalities: "C Tool use" (gestures involving a tool) and "NC Tool use" (non-communication tool-use actions)). All possible interactions between fixed variables were included at the beginning of the iterative model selection. Individual's identity was considered as a random variable to prevent pseudoreplication due to repeated observations.

CHAPTER 3

Captive chimpanzees' and gorillas' intraspecific gestural laterality

Article 1

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A multifactorial investigation of captive chimpanzees' intraspecific gestural laterality: implications for the origins of laterality at the population level and of human language

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Summary of Article 1

Questions: The study of non-human primates' laterality for intraspecific gestures in real-life social-ecological relevant contexts provides particularly valuable clues to enhance our understanding of the evolutionary relationship between population-level right-handedness and cerebral lateralization for human language. The goal of this study was to contribute to this understanding by investigating captive chimpanzees' intraspecific gestural laterality. Therefore, we analysed the most frequent gesture types of their communication repertoire and designed and applied a multifactorial approach to assess and to compare as rigorously as possible the respective influences of factors expected to modulate hand-preference. We wanted to answer the two following questions. Is there a gestural laterality bias at the population level? Which factors influence gestural laterality?

Methods: We studied intraspecific gestural laterality in dyadic interactions in three groups of chimpanzees (N=39) living under favourable captive conditions (when naturalization of enclosures is optimal and social groups include many subjects). We examined, first, each of 21 gestures separately. Second, we applied observational and statistical procedures considering simultaneously the following three categories of factors: interactional context components (visual field and body side of both signaller and recipient as well as the emotional valence of the context), gesture characteristics (sensory modality, use of a communication tool, degree of sharing, and duration), and individual sociodemographic characteristics of both signaller and recipient (age, sex, group/zoo, kinship, affiliation, and hierarchy).

Results: First, considering laterality on a continuum, 13 of the 21 gestures considered presented a right-hand bias at the population level. Second, results of a GLMM analysis evidenced that signallers' gestural laterality was influenced differently by several factors and their mutual intertwinement. More precisely, signallers used their hand ipsilateral to the recipient for tactile and visual gestures and their contralateral hand for gestures involving the auditory sensory modality and a communication tool. Signallers' right-hand use was more pronounced in negative contexts for common gestures as well as for subordinate signallers performing tactile gestures.

Conclusion: Our findings overall support the Ghirlanda and colleagues' (2009) model postulating that population-level biases could be explained by an evolutionary stable strategy based on intraspecific interactions. Our results also support the origin of human language theory stating that laterality in gestural communication represents a prerequisite of the language left-brain specialization. From an evolutionary point of view, our findings emphasize the importance to study intraspecific laterality in detail by applying a comparative approach using standardized methodologies including species varying in their degree of sociality, and taking into account multiple potentially influential factors and real-life social-ecological contexts.

A multifactorial investigation of captive chimpanzees' intraspecific gestural laterality: implications for the origins of laterality at the population level and of human language

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Abstract

Social laterality is the core of two major theories: one concerns the evolution of laterality at the population level and the other concerns the evolution of human language. However, few studies have investigated gestural laterality in communication between conspecifics. To our knowledge, the present study is the first to investigate the production of intraspecific gestures taking into account the influence of multiple factors on gestural laterality: first, gestural characteristics (sensory modality, use of a communication tool, sharing degree in the population and duration); second, the interactional context (visual field and body sides of signaller and recipient, and emotional context); and third, individual socio-demographic characteristics of signaller and recipient (age, sex, group, hierarchy, affiliation and kinship). We questioned, first, whether gestural laterality differed with gesture at the population level; second, whether some factors influenced gestural laterality. To do so, we evaluated social laterality in dyadic interactions in three groups of chimpanzees living in captivity (N=39). We found that, at the population level, 13 of the 21 gestures we observed were performed predominantly with the right hand. Gestural laterality of signallers was influenced mainly by interactional context, gesture characteristics (except gesture duration) and hierarchical rank of signaller. Signallers used their hand ipsilateral to recipients for tactile and visual gestures and their contralateral hand for gestures involving auditory communication and a communication tool. Moreover, signallers' use of their right hand was more important in negative contexts for gestures common to most of the subjects and by subordinates for tactile gestures. Our results further support the hypothesis that laterality in gestural communication might represent a precursor of the left-hemispheric lateralization of language. We discuss our results in relation to theories concerning the origins of cerebral hemispheric lateralization and their consistency with previous studies.

Keywords: social laterality, communication, gesture, chimpanzee, brain asymmetry.

Laterality in social behaviour is becoming an important research area as it is the core of two major theories: the first concerns the evolution of laterality at the population level (ELP) and the second concerns the origin of human language (OHL).

The ELP theory (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009) hypothesizes that the evolution of population-level asymmetries is influenced by social behaviour. Based on game-theory models, it suggests that behavioural laterality at the population level emerged in species subject to selection pressures imposed by social interactions rather than in solitary species. The OHL theory (Corballis 2002, 2003) hypothesizes an evolutionary relationship between the roots of human language and handedness. It postulates that the left-cerebral lateralization of language evolved from gestural communication. Below, we present arguments in favour of both theories.

Recent studies suggest that brain laterality is more ancient than previously expected (Vallortigara et al. 1999; Vallortigara 2006; MacNeilage et al. 2009). Brain and behaviour laterality at the population level, once thought to be specific to humans, has been evidenced in all vertebrate classes (i.e. fish: Sovrano et al. 1999; amphibians: Robins et al. 1998; reptiles: Deckel 1995; birds: Vallortigara 1992; and mammals: Casperd & Dunbar 1996; for a recent review, see Rogers et al. 2013) and several phyla of invertebrates (insects: Letzkus et al. 2006; arachnids: Heuts & Lambrechts 1999; malacostracans: Takeuchi et al. 2008, gastropods: Matsuo et al. 2010; cephalopods: Byrne et al. 2002; and nematodes: Hobert et al. 2002; for reviews, see Frasnelli 2013; Frasnelli et al. 2012a). These findings suggest that from an evolutionary point of view, lateralization contributes significantly to biological fitness. According to the theory of the evolution of laterality at the population level, brain lateralization may have evolved in two steps. First, biases at the individual level would have been selected because it brings advantages by increasing brain efficiency (e.g. review: Rogers et al. 2004). Second, biases at the population level (in populations including unequal numbers of left- and right-lateralized subjects) could have emerged from an Evolutionarily Stable Strategy (ESS)/frequency-dependent selection based on interspecific prey-predator interactions. This would have created advantages by coordinating behaviours of asymmetric organisms, but also disadvantages by making behaviours more predictable for predators and prey (e.g. shoaling fish: Vallortigara & Bisazza 2002). Ghirlanda and colleagues (2009) proposed that the pattern of population-level laterality could be explained by an ESS based on a trade-off between competitive and cooperative intraspecific interactions better than by interspecific interactions. Social laterality could have appeared at the population level because it facilitated intraspecific interactions (Rogers 2000). This has been evidenced for

invertebrates (e.g. spitting spiders: Ades & Ramires 2002, Heuts et al. 2003; red wood ants: Frasnelli et al. 2012b; fiddler crabs: Backwell et al. 2007) as well as for lower vertebrates (e.g. fish: Bisazza et al. 1999, 2000; amphibians: Robins et al. 1998, Vallortigara et al. 1998; birds: Vallortigara et al. 2001, Ventolini et al. 2005) and higher vertebrates (e.g. ungulates: Versace et al. 2007, Jennings 2012; cetaceans: Karenina et al. 2010, 2013; primates: Baraud et al. 2009, Meguerditchian et al. 2010).

Laterality of gestures in communication of our closest living relatives, the great apes, is the focus of an ever-growing body of research (e.g. Shafer 1987; Marchant & McGrew 1996; McGrew & Marchant 1997; Hopkins et al. 2012; Meguerditchian et al. 2013). These studies have nurtured recent scientific debates on the origins of language by providing arguments in favour of the gesture-first view (Arbib et al. 2008; Corballis 2002, 2003; McNeill 2012). From now on, we will refer to gestures as "movements of the limbs or head and body directed towards a recipient that are goal-directed, mechanically ineffective (that is, they are not designed to act as direct physical agents) and receive a voluntary response" (Pika & Bugnyar 2011; p 4). A first argument supporting the gesture-first view is that non-human primates' gestural communication is very flexible in relation to factors such as social context, hierarchical rank, age, population and species (e.g. Maestripieri 1999; Call & Tomasello 2007; Pika et al. 2005a; Pika 2008a, Arbib et al. 2008). This variation seems to be due to three complementary mechanisms: phylogenetic ritualization, ontogenetic ritualization and social learning (Tinbergen 1952; Liebal & Call 2012; Tomasello et al. 1997). A second argument is provided by the recent discovery of monkeys' and humans' so-called mirror neurons that presumably exist in all primate brains (see review: Fabbri-Destro & Rizzolatti 2008). As shown by Gallese and colleagues (1996) for rhesus monkeys, mirror neurons are neurons that discharge both when a subject acts and when it observes the same action being performed by another subject. They are located in area F5, which is homologous to humans' language production area (e.g. Nishitani & Hari 2000). The study of hemispheric specialization for communication shows a predominance, in humans' left cerebral hemisphere, of Broca's area (responsible for speech production) and Wernicke's area (responsible for understanding speech) (Horwitz et al. 2003; Xu et al. 2009) and of homologous areas in great apes (Gannon et al. 1998; Cantalupo & Hopkins 2001; Cantalupo et al. 2003; Hopkins et al. 2007; Spocter et al. 2010; Hopkins & Nir 2010). Correlatively, observations of apes in captivity revealed that communication gestures were expressed mainly via the right hand (e.g. Hopkins et al. 2012). A third argument stresses the deep intertwinement between humans' spoken language and gesture laterality with a predominant use of the right hand for (i) speech-accompanying

gestures (e.g. Kimura 1973), (ii) sign language by deaf speakers (e.g. Bellugi 1991; Corina et al. 1992) and (iii) pre-linguistic gestures (e.g. Blake 2000; Vauclair & Imbault 2009). A fourth argument is that non-human primates' gestural communication system shares several key characteristics with human language such as intentionality (e.g. Call & Tomasello 2007; Meguerditchian & Vauclair 2006; Meunier et al. 2012; Maille et al. 2012; Bourjade et al. 2014) and referential properties (e.g. imperative POINTING[16]: Leavens & Hopkins 1999; DIRECTED SCRATCHES: Pika & Mitani 2006; BECKONING: Genty & Zuberbühler 2014). All these properties underlying the production and use of sophisticated gestural communication are crucial prerequisites for human language.

In addition, many other factors (i.e. gesture type, production of vocalizations, relative positions of subjects during an interaction, emotional valence and socio-demographic components) have been found to modulate laterality expressed in gestural communication. For instance, Hobaiter and Byrne (2013) showed that chimpanzees in the wild use their right hands significantly more for object-manipulation gestures than for non-object-manipulation gestures. Hopkins and colleagues (Hopkins & Leavens 1998; Hopkins & Wesley 2002) showed that captive chimpanzees used their right hands more for begging humans than for pointing at them. Moreover, chimpanzees who vocalized during trials were more likely to use their right hand than those that did not vocalize (Hopkins & Leavens 1998; Hopkins & Cantero 2003; Hopkins et al. 2005a). Therefore, the nature of chimpanzees' gestures seems to have a crucial impact on the direction and strength of hand use during communication. This could explain discrepancies between studies focusing on different gestures.

Surprisingly, relatively little is known about the impact of the position of the recipient (most often a human) on primates' hand-preference. To date, authors report the influence of the experimenter's position on hand use for FOOD BEG and POINTING (pooled data) by chimpanzees (Hopkins & Wesley 2002), but not on captive baboons' hand preference for food-begging tasks (Bourjade et al. 2013). Concerning the emotional valence of the context, Basile and colleagues (2009) showed that only negative voices (defined as conspecific sounds having a negative emotional value) induced auditory laterality in Campbell's monkeys and human girls. Intraspecific agonistic interactions generally induce a preferential use of the left visual field by many vertebrates (e.g. toads: Vallortigara et al. 1998; lizards: Deckel 199; chicks: Vallortigara et al. 2001; adult hens: Rogers 1991; horses: Austin & Rogers 2012; baboons: Casperd & Dunbar 1996). Differently, Chapelain and colleagues (in prep.) found a

[16] Gestures are depicted in lower capitals

left visual field bias for bonobos' positive interactions. Three species of fish (Bisazza & de Santi 2003) and deer (Jennings 2012) aggressed conspecifics using mainly the right side of their body. These studies highlight complex interactions between the respective positions of signaller and recipient (for both body side and visual field) and the emotional context, interactions that require further investigations to understand better their influence on primates' gestural communication with conspecifics.

Concerning sociodemographic factors, a few studies investigated the effect of age. Chimpanzees' right direction in hand preference increased with age in the wild (Hobaiter & Byrne 2013) and in captive environments (Hopkins & Leavens 1998). However immature Przewalski horses' strength of eye preference towards the left was stronger than that of adults when looking bouts concerned an attack or vigilance (Austin & Rogers 2014). Regarding sex effect, as far as we know, only two studies have reported such effect in gestures with however opposite results: Hopkins and Leavens (1998) found that male chimpanzees tended to be less right-handed than females, whereas Hopkins and de Wall (1995) found that male bonobos were more right-handed than females. Other studies did not evidence an influence of sex on non-human and human primates' laterality in gestures (chimpanzees: Hopkins et al. 2005a; baboons: Meguerditchian & Vauclair 2009, Meguerditchian et al. 2011; humans: Sommer & Kahn 2009). Concerning social factors, hierarchical rank effects on laterality have been investigated only in non-human primates. Baraud and colleagues (2009) showed that rank influenced mangabeys' approach side as well as relative transversal and vertical positions: high-ranking subjects were approached more often from their left than from their right. To our knowledge, only one study has investigated kinship effect in gestures: Hopkins and colleagues' (2005b) studying captive chimpanzees' hand preference for THROWING directed towards both humans and conspecifics (pooled data) did not show an influence of kinship. The influence of affiliation remains undocumented. No effects of communication type (intraspecific versus interspecific: Meguerditchian & Vauclair 2006; Meguerditchian et al. 2010, 2011) or of rearing history (mother-reared, nursery reared, wild caught: Hopkins et al. 2005a) on captive chimpanzees' gestural communication have been evidenced. Taking into consideration these findings, we argue that population-level handedness in communication is not a consequence of captive environment and human presence and that the full range of individual sociodemographic characteristics must be taken into consideration all together to assess their relative weights and possible influences on primates' gestural communication.

These findings emphasize the importance of studying non-human primates' gestural communication to improve our understanding of the origin and evolution of both social

laterality and language. To our knowledge, no previous study has assessed gestural laterality using a comprehensive approach taking into account simultaneously multiple influential factors and their interactions as well as considering sociodemographic characteristics and narrow categories of age (e.g. immature, adolescent, young and mature adult and elder) and hierarchy (e.g. dominant, intermediate and subordinate) of both signaller and recipient, essential requirements to avoid biases and to yield unambiguous results. Whereas many studies investigated non-human primates' gestural communication in artificial situations with human experimenters (see review: Meguerditchian et al. 2013), only a few studies analyzed gestural complexity during spontaneous communication strictly between conspecifics in captivity (chimpanzees: Fletcher & Weghorst 2005; Meguerditchian et al. 2010; bonobos: Chapelain 2010; baboons: Meguerditchian & Vauclair 2006) or in the wild (chimpanzees: Pika & Mitani 2006; Hobaiter & Byrne 2013). Socio-ecologically relevant conditions close to conditions where natural selection has acted are of particular interest to study gestural laterality in an evolutionary perspective.

Therefore, the main aim of this study was to understand better intraspecific gestural laterality and the factors influencing hand-preferences in one of humans' closest living relatives, chimpanzees (*Pan troglodytes*). To this end, we investigated systematically the production of the most frequent gesture types of their communication repertoire (e.g. Nishida et al 1999, 2010). We designed and applied a methodology to assess and to compare as unambiguously as possible the respective influences of factors expected to modulate laterality in gestural communication. Our first question was: Is there a gestural laterality bias at the population level[17]? To answer this question, we analysed each of 21 gestures separately. As seen in human literature (e.g. Kimura 1973), we predicted that a majority of these frequently expressed gestures would be right-lateralized at the population level. Our second question was: which factors influence gestural laterality? To answer this question, the three following categories of factors were taken into account simultaneously: the interactional context components (visual field and body side of both signaller and recipient and the emotional valence of the context), gesture characteristics (sensory modality, use of communication tool, degree of sharing and duration) and individual sociodemographic characteristics of both signaller and recipient (age, sex, group, hierarchy, kinship and affiliation). Based on the reports mentioned above, we predicted that signallers' gestural laterality would be particularly

[17] In this study our population includes all our subjects.

modulated by interactional context, gesture characteristics and individual social characteristics.

Methods

Subjects

Thirty-nine chimpanzees raised under semi-natural conditions were observed in three zoos: Leipzig Zoo (Germany), Beauval Zoo and La Palmyre Zoo (France). Following Goodall (1986) age categories of the subjects were defined as follows: immatures (0–7 years old), adolescents (8–12 years old), young adults (13–20 years old), mature adults (21–35 years old), and elderly (over 35 years old) (Table 1).

Observation procedures

Observation data were collected at the Wolfgang Köhler Primate Research Center at the Leipzig Zoo between the 1st of July and the 20th of September 2013, at Zooparc de Beauval between the 29th of September and the 10th of November 2013 and at La Palmyre Zoo between the 23th of November and the 22th of December 2013. This yielded respectively 333 h, 198 h and 174 h of observations, for a total of 705 h.

During observation days, data were collected during four 1.5h sessions, two in the morning and two in the afternoon. The sampling rule was "sampling all occurrences of some behaviours" (Altmann 1974) to optimize data recording, and particularly not to miss infrequent gestures such as EMBRACE HALF or THROW. Data were collected in real time by using a stopwatch, binoculars, and a paper sheet onto which observation data were recorded.

Coding procedure

Only dyadic interactions were taken into account. We defined the individual that started the social interaction as the signaller and the target of this interaction as the recipient. For each dyadic interaction, we recorded (1) the type of gesture (based on Nishida and colleagues.' ethograms, 1999, 2010) and the left or right limb (hand or foot) used by the signaller to communicate, (2) the interactional context of gestural production recording the relative positions of the two subjects before and during an interaction (both visual field and

body side) as well as the emotional context associated with the interaction, and (3) the identity and role (signaller or recipient) of both subjects, as described below.

Following Pika's definition of gesture (Pika 2008a, 2008b), we considered only intentionally produced gestures that (1) were used to initiate (not continue) a social interaction, (2) were mechanically ineffective (a gesture that "visibly lacks the mechanical force to bring about the reaction shown by the recipient, and also does not include any attempt to grab or extensively hold a body part of the other": Pollick & de Waal 2007, p. 8185), (3) and included gazing at the recipient, gaze alternation, and/or waiting for a response (e.g. Bruner 1981; Tomasello et al. 1989).

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

Data were recorded when a gesture was produced either singly or in a gesture bout (i.e. sequence of gestures separated by intervals) (e.g. Marchant & McGrew 1991; Byrne & Byrne 1991). Only the first gesture of a bout was recorded. The following criteria must be met to consider that a single gesture or a bout was terminated: the signaller's hand (a) returned to its initial position (Meguerditchian et al. 2010), (b) switched to another non-communication activity (e.g. forage), or (c) the movement was influenced by an outside incident (e.g. stumble) (Hopkins & de Waal 1995; Hopkins et al. 2001a; McGrew & Marchant 2001, Harisson & Nystrom 2010). A change in hand activity must last more than 3 seconds before another gesture can be taken into account thus ensuring statistical independence of data (Morris et al. 1993; Hopkins & de Waal 1995).

Gesture characteristics

Our gesture classification was based on previous gestural repertoires (when necessary anatomical elements or precisions were added) (Tables 2 and 3). Twenty-one different gestures were considered and divided into three communication modalities: visual gestures that generate a mainly visual component with no physical contact (n=7), auditory gestures that generate sound while being performed (n=3) or tactile gestures that include physical contact with the recipient (n=11) (following Pika et al. 2003, 2005). These gestures were performed either with (n=5) or without (n=16) an object used as a communication tool. We measured the time subjects took to perform a single gesture: the starting point was determined by a hand

starting to move, the end point when the hand was again in a resting position (Kendon 1980; McNeill 1992). Gestures lasting less than 2 seconds were categorized as "short" gestures (n=12) and gestures lasting more than 2 seconds were categorized as "long" gestures (n=9). Gestures were also divided as follows: eight of the 21 gestures, each performed by less than 14 subjects, were categorized as "rare" gestures, defined as gestures performed by only a few subjects in our population (represented by our 39 subjects) and the 13 other gestures performed by at least 25 subjects were categorized "common" gestures, defined as gestures performed by most of the subjects in the population.

Characteristics of the interactional context of gestures production

For each dyadic interaction, we recorded the relative positions – visual field used and exposed body side – of both subjects before (the last position for 2 seconds before an interaction) and during the interaction. Most interactions were predictable as signallers emitted intentional signals (e.g. gazing at the recipient, gaze alternation, movement towards the recipient).

The emotional contexts of interactions were divided into two categories – positive and negative – according to three criteria. The emotional context was primarily based on the response of the recipient, but also on the associated global social context and on the signallers' expressions if necessary. The emotional context was inferred according to (1) the functional consequences of the gesture during an interaction (the response of the recipient to the signaller's gesture). The possible responses of the recipient were: apparent change of the recipient's behaviour including communication responses (via gestural, vocal, facial and/or whole-body expressions) or actions (modification of activity - change or stop -, modification in possession of a resource), or no apparent change in the recipient's behaviour; (2) the global social context in which the given interaction occurred: aggression, post-conflict reconciliation (contact between former opponents) and consolation (contact of the aggressed party with a third animal), access to food, object or infant, nursing, grooming, mating, play and travel; (3) the signaller's facial (Parr & Waller 2006; Parr et al. 2005) and vocal (Crockford & Boesch 2005) expressions and, to a lesser extent, whole-body expressions (e.g. rhythmic movements: Goodall 1989; pilo-erection: Van Hooff 1973; Goodall 1989).

Sociodemographic characteristics of the subjects

In addition to individual demographic characteristics, such as age and sex, we considered data concerning kin and social relationships (affiliation and hierarchy).

Kinship

Kinship was determined by genetic analyses and data were provided by each zoo. Three categories of chimpanzee pairs were considered: (1) "Parent-infant" including mother-infant and father-infant pairs, (2) "Siblings" including siblings and half-siblings, and (3) "Unrelated" for pairs of genetically unrelated subjects.

Affiliation

According to Pollick and de Waal's (2007) definition of affiliative and agonistic behaviours we selected the following six strict affiliative gestures (gestures that are expressed only in positive contexts; 8986 interactions in total) to quantify affiliation: EMBRACE, EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, EXTEND HAND, and TOUCH BODY. We analysed all agonistic interactions recorded (4334). These interactions include the mechanically ineffective gestures considered in this study but also SLAP BODY and SLAP (Pika et al. 2003) that we did not retain because data concerning these actions did not meet the statistical criteria required for the binomial test (see details below in Descriptive statistics) and two mechanically effective gestures: GRAB and PUSH (mechanical effective version) (Pika et al. 2005a). Two indexes of interest have already been used to evaluate relationship quality (Weaver & de Waal 2002; Silk et al. 2013). To remedy disadvantages of these two indexes and to better evaluate relationship quality within pairs of individuals (Prieur 2015), we created a Dyadic Affiliation Index (DAI) to assess relationship quality based on the relative frequencies of affiliative and agonistic behaviours within the dyad. This index increases with affinity, starting from 0 in absence of affinity. It is calculated as:

$$DAI_{xy} = \frac{\left(\frac{\sum_{i=1}^{n} \frac{f_{ixy}}{\bar{f}_i}}{n}\right)}{1 + \left(\frac{\sum_{j=1}^{n'} \frac{h_{jxy}}{\bar{h}_j}}{n'}\right)}$$

Where f_{ixy} is the total number of affiliative interactions of the behaviour (*i*) expressed by *x* towards *y*; $\bar{f}_i$ is the mean number of affiliative interactions of the behaviour (*i*) across all dyads; *n* is the number of affiliative behaviours expressed by *x* towards *y*; h_{jxy} is the total number of agonistic interactions of the behaviour (*j*) expressed by *x* towards *y*; $\bar{h}_j$ is the mean number of agonistic interactions of the behaviour (*j*) across all dyads; *n'* is the number of agonistic behaviours expressed by *x* towards *y*. Three categories of dyadic affiliation were considered: (1) "Low" from 0 to 0.5 (389 dyads), (2) "Medium" from 0.5 to 1 (58 dyads), and (3) "High" more than 1 (47 dyads).

Hierarchy

Following Langbein and Puppe (2004), hierarchical dominance relationships were determined on the basis of agonistic interactions (Pollick & de Waal 2007). Only interactions within dyads for which the aggressor and the receiver of the threat were clearly identified were taken into account.

All recorded agonistic interactions (4334) were considered. We organized these interactions into sociometric matrices from which we calculated Kendall's coefficient of linearity *K*, Landau's linearity index *h* and the index of linearity *h'* (de Vries 1995), using MatMan 1.1 (Noldus Information Technology, Wageningen, Netherlands). The index *h'* is based on *h* and takes into account the existence of unknown relationships (when two subjects of a dyad had not been observed to interact aggressively with each other or when they had an equal number of wins and losses). Each index varies from 0 (absence of linearity) to 1 (complete linearity). Statistical significance of *K* was provided by a chi-square test. A resampling process using 10 000 randomizations was performed for the *h'* index (de Vries 1995). When the dominance hierarchy was significantly linear, subjects were reordered by a two-step iterative procedure, finding the rank order most consistent with a linear hierarchy by minimizing the number of inconsistencies and then minimizing the total strength of the inconsistencies (de Vries 1998; de Vries et al. 2006). Each of the N subjects in one zoo was then assigned a rank from 1 (the most dominant) to N (the most subordinate). Three categories of hierarchical rank were considered: "Subordinate", "Intermediate", and "Dominant" (Beauval group: 5 subordinates, 5 intermediates and 4 dominants; Leipzig group: 5 subordinates, 5 intermediates and 6 dominants; Palmyre group: 3 subordinates, 3 intermediates and 3 dominants).

Statistical analysis

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.

Descriptive Statistics

To enable subsequent statistical analyses (binominal test), we included data only for gestures that had been recorded at least six times each by at least six subjects (Chapelain 2010).

Binomial tests on the numbers of responses involving the left and right hands assessed individual-level biases for each gesture. Direction of gestural asymmetry was evaluated by calculating an individual Handedness Index (HI) for each subject applying the formula HI= (R-L)/(R+L), where R and L represent the total number of right- and left-hand responses respectively. HI varies from -1.0 to +1.0. Its sign indicates direction of hand preference, positive values correspond to a right-hand preference and negative values to a left-hand preference. The strength of individual hand preference was estimated by the absolute value of HI (ABSHI). This procedure is similar to that used by previous authors (e.g. Harris & Carlson 1993; Hopkins 1995).

Binomial tests assessed population-level biases in the number of lateralized and non-lateralized subjects for each gesture. When at least six subjects were lateralized, binomial tests assessed population-level biases in the number of right-handers and left-handers for each gesture. We evaluated the bias in hand use at the population level by a one-sample two-sided Student's t-test on the HI values of all subjects only when the HI distribution was normal (Shapiro-Wilk normality test) and by a one-sample Wilcoxon signed rank test when the HI distribution was not normal.

Spearman correlation tests estimated potential effects of the number of data points per subject on the direction and strength of laterality. Pearson correlation tests checked possible correlations between the visual field and body side of both signaller and recipient as well as before and during an interaction.

Generalized Linear Mixed Model analysis on the multiple influential factors

We evaluated the possible effect of multiple variables on gestural laterality using a generalized linear mixed model (GLMM) for binary data (logistic regression) with hand use as the dependent variable. This GLMM analysis allowed estimation of the effects of

interactional context as well as gesture and individual sociodemographic characteristics on hand use (see Table 4 for a descriptive summary of dependent, fixed and random variables).

The fixed variables were: position (Left or Right) of the recipient in the signaller's visual field during the interaction (noted SVF), position of the signaller in the recipient's visual field during the interaction (RVF), emotional context, gesture characteristics (sensory modality: auditory, tactile or visual; use of communication tool: with or without object, sharing degree: common or rare; duration: short or long) as well as social (kinship, hierarchy, dyadic affiliation) and demographic (age, sex, zoo) characteristics. We included all possible interactions between fixed variables.

To avoid pseudoreplication caused by repeated observations (Waller et al. 2013), we considered signallers' and recipients' identities as the random variables. For the GLMM analysis, we used the 'glmer' function ['lme4' package (Bates et al. 2014)] and 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 'Anova' function ['car' package (Fox & Weisberg 2011]. Least Square means (LSmeans) and associated adjusted probabilities of right-hand use were computed using 'lsmeans' function ['lsmeans' package (Lenth 2014)]. Post-hoc multiple comparisons tests were performed using Tukey's HSD test and calculated between LSmeans ('lsmeans' package).

Results

We recorded 25 534 gesture occurrences during 705 hours observation. After having applied the statistical criteria required for performing the binomial test (Siegel & Castellan 1988), 25 024 gesture occurrences were retained for descriptive statistics and related analyses. The mean number of gesture occurrences per subject was 641.641 (min=29, max=3 198; SD=764.162).

Gestural laterality at the population level

To estimate gestural laterality at the population level, we analysed each of the 21 gestures separately. Significantly more subjects were non-lateralized than lateralized for 8 tactile and 2 visual gestures (binomial test: tactile gestures: $P \leq 0.008$; visual gestures: $P \leq$

0.023; Table 3), the average percentage of non-lateralized subjects for all gestures was 66.862% (min=12.5, max=100, SD=22.466).

Analyses revealed that significantly more subjects were right-handed than left-handed for the 6 following gestures (binomial test: $P \leq 0.001$; Table 3): two auditory (SLAP HAND and SLAP FOOT), one tactile (PUNCH), and three visual gestures (SHAKE OBJECT, EXTEND HAND and RAISE ARM). We evidenced a significant right-hand bias at the population level for 13 gestures (one-sample two-sided t-test or one-sample Wilcoxon signed rank test, $P \leq 0.024$; Table 3). The average Mean HI was 0.213 (min=-0.151, max=0.471; SD=0.193) and the average Mean ABSHI was 0.362 (min=0.149, max=0.836; SD=0.162) for all the 21 gestures.

We found a significant effect of the number of data points per subject on the HI and ABSHI values for each gesture only for PUSH for which a positive correlation was found (Spearman correlation test: N = 24 HI: r_s=0.425, P = 0.039, ABSHI: r_s=0.452, P = 0.026) and for TOUCH BODY for which a negative correlation was found for ABSHI (Spearman correlation test: r_s=-0.469, P = 0.003, N = 39) (Appendix Table A1).

Factors and their mutual interactions influencing gestural laterality

To evidence factors influencing gestural laterality, we focused on interactional context components, gesture characteristics, and individual sociodemographic characteristics. We carried out a GLMM analysis taking into account all the 25 534 gesture occurrences. The mean number of gesture occurrences per subject associated was 654.718 (min=47, max=3 199; SD=758.797).

The different visual field combinations of both signaller and recipient during an interaction are schematized in Figure 1 with the corresponding percentages of occurrences. The results showed that the direction of the visual fields of both signallers and recipients were similar in 36.2% of the occurrences (Figs. 1a and 1b) and opposed in 63.8% of the occurrences (Figs. 1c and 1d). This relationship was confirmed by a weak negative correlation but highly significant between the signaller's and the recipient's visual fields during interaction (Pearson's rank correlation: r_p = - 0.28, $P < 0.0001$, n = 25 456).

Independent of role (signaller or recipient), the visual field in which the partner was located coincided with the body side exposed towards this partner, before a given interaction on the one hand (signaller: Pearson's rank correlation: r_p = 0.99, $P < 0.0001$, n = 25 413; recipient: Pearson's rank correlation: r_p = 0.99, $P < 0.0001$, n = 25 405), and during this

interaction on the other hand (signaller: Pearson's rank correlation: $r_p = 0.98$, $P < 0.0001$, $n = 25\,464$; recipient: Pearson's rank correlation: $r_p = 0.99$, $P < 0.0001$, $n = 25\,456$).

Furthermore, independent of role (signaller or recipient) the visual fields in which the partner was located before and during an interaction were strongly positively correlated (signaller: Pearson's rank correlation: $r_p = 0.70$, $P < 0.0001$, $n = 25\,412$; recipient: Pearson's rank correlation: $r_p = 0.86$, $P < 0.0001$, $n = 25\,404$).

These strong positive correlations enabled reduction of the number of position variables in the GLMM analysis by retaining only the signaller's and recipient's visual fields during an interaction.

The analysis of deviance results corresponding to the best GLMM model are presented in Table 5. The result corresponding to a given variable (considered separately) was accounted for only when this variable was not involved in significant interactions with other variables. This was the case only for "Recipient's sex", for which a moderate trend towards significance was found. Variables for which a significant or trend significant interaction was found (Table 5) were considered successively: interactional context variables (signaller's visual field, recipient's visual field and emotional context), gesture characteristic variables (sensory modality, use of communication tool, sharing degree, duration) as well as social (kinship, hierarchy, dyadic affiliation) and demographic (age, sex, zoo) variables. Results of post-hoc multiple comparisons tests are presented in Appendix Table A2. Table 6 presents a summary of the results. For clarity, only significant and trend p-values are given in the text below whereas all p-values are presented in Table A2.

Influence of interactional context on gestural laterality

Influence of the position of the recipient in the signaller's visual field during an interaction (SVF). Signallers used their right hand more when the recipient was in their right visual field (SVF_R) than in their left visual field (SVF_L) during an interaction for tactile and visual gestures (Fig. 2a), gestures without object (Fig. 3a) as well as short and long gestures (Tukey test: for each of these variable modalities: $P < 0.0001$). This was also true whatever the signaller's hierarchical rank (Fig. 4a), the recipient's age class and the zoo (Tukey test: for each of these variable modalities: $P < 0.0001$). On the contrary, signallers used their right hand more when the recipient was in their left visual field (in SVF_L condition) than in their right visual field (SVF_R) for auditory gestures (Fig. 2a) (Tukey test: $P < 0.0001$). No evidence of SVF influence was found for gestures with object (Fig. 3a) (Tukey test: $P = 0.292$).

Influence of the position of the signaller in the recipient's visual field during an interaction (RVF). Signallers used their right hand more when they were in the recipient's left visual field (RVF_L) than in their right visual field (RVF_R) during an interaction for tactile and auditory gestures (Fig. 2b), gestures with and without object (Fig. 3b) as well as short and long gestures (Tukey test: tactile: $P < 0.0001$; auditory: $P < 0.0001$; with object: $P = 0.009$; without object: $P < 0.0001$; short: $P = 0.015$; long: $P < 0.0001$). This was also true for parent-infant and unrelated pairs, the three youngest signaller age classes (immatures, adolescents and young adults, Fig. 6a), and whatever the signaller's hierarchical rank (Fig. 4b) and the zoo (Tukey test: parent-infant and unrelated pairs: $P < 0.0001$; immature: $P = 0.003$; adolescent: $P < 0.0001$; young adult: $P < 0.0001$; dominant: $P < 0.0001$; intermediate: $P = 0.025$; subordinate: $P < 0.0001$; Beauval, Leipzig and La Palmyre: $P < 0.0001$). This laterality pattern was not statistically disproved for the remaining variable modalities: visual gestures (Fig. 2b), siblings and the two oldest signaller age classes (mature adults and elders, Fig. 6a) (Tukey test: visual: $P = 0.741$; siblings: $P = 0.257$; mature adult: $P = 0.794$; elder: $P = 0.728$).

Influence of the emotional context. Signallers were more right-handed in negative than in positive contexts only when performing common gestures (Fig. 5) (Tukey test: $P = 0.018$). No influence of emotion on rare gestures (Fig. 5) whatever the gesture sensory modality, the gesture duration or whether a tool was used or not, was evidenced.

Influence of gesture characteristics on gestural laterality

Influence of the gesture sensory modality. Signallers used their right hand more for visual than for auditory gestures when the recipient was in their right visual field (SVF_R) (Fig. 2a) and when the signaller was in the recipient's right visual field (RVF_R) (Fig. 2b), for rare gestures, dominant and intermediate signallers (Fig. 7a), immature, young adult and elder signallers as well as for the Leipzig and Beauval groups (Tukey test: SVF_R: $P < 0.0001$; RVF_R: $P < 0.0001$; rare: $P < 0.0001$; dominant: $P < 0.0001$; intermediate: $P = 0.037$; immature: $P = 0.0001$; young adult: $P = 0.005$; elder: $P = 0.012$; Leipzig: $P < 0.0001$; Beauval: $P = 0.020$) (this laterality pattern was not statistically disproved for the remaining variable modalities: common gestures, subordinate signallers, adolescents signallers and Palmyre group). This was also true whatever the emotional context, the recipient's hierarchical rank (Fig. 7b) and the signaller's sex (Tukey test: positive and negative emotion: $P < 0.0001$; subordinate: $P < 0.0001$; intermediate: $P = 0.0050$; dominant: $P < 0.0001$; female: $P < 0.0001$; male: $P = 0.001$). Moreover, this tended to be marginally true for RVF_L

situation and for mature adult signallers (Tukey test: RVF_L: $P = 0.087$; mature adult: $P = 0.096$). On the contrary, signallers tended to use their right hand more for auditory than for visual gestures for SVF_L (Tukey test: SVF_L: $P = 0.059$)

Signallers used their right hand more for visual than for tactile gestures when the recipient was in their left visual field (SVF_L) (Fig. 2a) and when the signaller was in the recipient's right visual field (RVF_R) (Fig. 2b), in positive emotional contexts as well as for common gestures, dominant signallers (Fig. 7a) and recipients (Fig. 7b), immature and elder signallers, female signallers and Leipzig group (Tukey test: SVF_L: $P = 0.0009$; RVF_R: $P < 0.0001$; positive emotion: $P < 0.0001$; common: $P < 0.0001$; dominant signaller: $P < 0.0001$; dominant recipient: $P = 0.003$; immature signaller: $P = 0.048$; elder signaller: $P = 0.0007$; female signaller: $P < 0.0001$; Leipzig: $P < 0.0001$) (this laterality pattern was not statistically disproved for the remaining variable modalities).

Signallers used their right hand more for tactile than for auditory gestures when the recipient was in their right visual field (SVF_R) (Fig. 2a) as well as when the signaller was in the recipient's left visual field (RVF_L) (Fig. 2b), in negative emotional contexts, for rare gestures, dominant signallers (Fig. 7a), dominant and subordinate recipients (Fig. 7b), young and mature adult signallers, male signallers and for the Leipzig group (Tukey test: SVF_R: $P < 0.0001$; RVF_L: $P = 0.0013$; negative emotion: $P = 0.001$; rare: $P < 0.0001$; dominant signaller: $P = 0.006$; dominant and subordinate recipients: $P = 0.008$; young adult signaller: $P = 0.025$; mature adult signaller: $P = 0.031$; male signaller: $P < 0.012$; Leipzig: $P < 0.0001$). This tended to be marginally true for RVF_R situation as well as moderately true for female signallers (Tukey test: RVF_R: $P = 0.087$; female signaller: $P = 0.065$). This laterality pattern was statistically disproved only for SVF_L situation (Fig. 2a) and for common gestures for which signallers used their right hand more for auditory than for tactile gestures (Tukey test: SVF_L: $P < 0.0001$; common: $P = 0.0003$).

Influence of the use of communication tools in gestures. Signallers used their right hand for gestures without object more than for gestures with object when the recipient was in their right visual field (SVF_R) (Fig. 3a) as well as when the signaller was immature, adolescent or elder (Tukey test: SVF_R: $P < 0.0001$; immature signaller: $P = 0.0004$; adolescent signaller: $P = 0.034$; elder signaller: $P < 0.0001$). This was also true whatever their location in the recipient's visual field (RVF) (Fig. 3b) and the emotional context (Tukey test: RVF_L: $P = 0.019$; RVF_R: $P < 0.0001$; negative and positive emotion: $P < 0.0001$). On the contrary for SVF_L situation signallers used their right hand more for gestures with object than without

object (Fig. 3a) (Tukey test: $P < 0.0001$). We did not evidence an influence of the use of a communication tool on right-hand use for young and mature adult signallers.

Influence of gesture sharing degree. Signallers used their right hand more for common than for rare gestures in negative emotional contexts (Fig. 5) as well as when they were dominant or immature, for auditory gestures, for gestures directed towards a strong affiliative partner and for the Palmyre group (Tukey test: negative emotion: $P = 0.021$; auditory: $P < 0.0001$; dominant signaller: $P = 0.025$; immature signaller: $P < 0.0001$; strong affiliative partner: $P = 0.043$; Palmyre: $P = 0.006$). They also tended to use marginally their right hand more for common than for rare gestures directed towards a low affiliative partner (Tukey test: low affiliative partner: $P = 0.091$). This laterality pattern was statistically disproved only for tactile gestures for which signallers used their right hand more for rare gestures than for common gestures (Tukey test: $P = 0.042$).

Influence of gesture duration. Signallers used their right hand more for long than for short gestures when the signaller was in the recipient's left visual field (RVF_L) (Tukey test: $P = 0.037$) and this was not disproved for RVF_R situation. On the contrary, signallers used their right hand more for short than for long gestures in positive emotional contexts (Tukey test: $P = 0.008$) (this laterality pattern was not statistically disproved in negative emotional contexts). No evidence of an influence of gesture duration on signaller's right-hand use was found whatever the position of the recipient in the signaller's visual field (SVF).

Influence of individual social characteristics on gestural laterality

Influence of the signaller's hierarchical rank. Subordinate signallers used more their right hand than intermediate signallers when the recipient was in their left visual field (SVF_L) (Fig. 4a) as well as when the signaller was in the recipient's left visual field (RVF_L) (Fig. 4b), for tactile gestures (Fig. 7a), rare gestures, and gestures directed towards a medium affiliative partner (Tukey test: SVF_L: $P = 0.020$; RVF_L: $P = 0.025$; tactile: $P = 0.021$, rare: $P = 0.017$; medium affiliative partner: $P = 0.026$). This tended to be marginally true for gestures directed towards a low affiliative partner (Tukey test: $P = 0.095$). Furthermore, subordinate signallers used more their right hand than dominant signallers in SVF_R situation (Fig. 4a), as well as for rare gestures, and when performing gestures towards a medium affiliative partner (Tukey test: SVF_R: $P = 0.023$; rare: $P = 0.040$; medium affiliative partner: $P = 0.011$). They tended to use their right hand more than dominant signallers in RFV_R

situation (Fig. 4b), for tactile gestures (Tukey test: RVF_R: $P = 0.091$; tactile: $P = 0.068$). No influence of signaller's hierarchical rank on right hand use was evidenced for auditory and visual gestures (Fig. 7a), common gestures and gestures directed towards low or strong affiliative partners.

Influence of the recipient's hierarchical rank. We did not evidence an influence of recipients' hierarchical rank on signallers' right-hand use for any of the gesture sensory modalities (Fig. 7b).

Influence of kinship. When signallers were located in the recipient's left visual field, they tended to be more right-handed for gestures towards an unrelated recipient than towards a sibling recipient (Tukey test: $P = 0.068$).

Influence of affiliation. Subordinate signallers were less right-handed when performing gestures towards a strong affiliative subordinate partner than towards a medium partner (Tukey test: $P = 0.018$). No evidence of affiliation effect on signallers' right-hand use was found for dominant and intermediate signallers as well as whatever the degree of gesture sharing and the signaller's age class.

Influence of individual demographic characteristics on gestural laterality

Influence of signaller's age class. Elder signallers were less right-handed than mature adult signallers for rare gestures, as well as whatever their location in the recipient's visual field during the interaction (RVF) (Fig. 6b), gesture sensory modality, use of a communication tool or not and affiliation of the recipient (Tukey test: rare: $P < 0.001$; RVF_R: $P < 0.0001$; RVF_L: $P < 0.0001$; tactile: $P < 0.0001$; auditory: $P = 0.010$; visual: $P = 0.002$; without object: $P = 0.010$; with object: $P < 0.0001$; strong affiliative partner: $P = 0.001$; medium affiliative: $P < 0.001$; low affiliative: $P = 0.0004$). They were less right-handed than young adult signallers for tactile gestures and gestures with an object, gestures directed towards medium and low affiliative partners, whatever RVF situation (Fig. 6a) and the degree of gesture sharing (Tukey test: tactile: $P < 0.0001$; with object: $P < 0.0001$; medium affiliative partner: $P = 0.002$; low affiliative: $P = 0.005$; RVF_R: $P = 0.024$; RVF_L: $P < 0.0001$; rare: $P = 0.004$; common: $P = 0.009$). This tended to be moderately true for visual gestures (Tukey test: $P = 0.071$). Elder signallers were also less right-handed than adolescent signallers for tactile and auditory gestures, gestures with object, gestures directed towards medium and

strong affiliative partners, whatever RVF (Fig. 6b) and the degree of gesture sharing (Tukey test: tactile: $P < 0.0001$; auditory: $P = 0.006$; with object: $P < 0.0001$; strong affiliative: $P = 0.034$; medium affiliative partner: P = 0.0002; RVF_R: $P = 0.042$; RVF_L: $P < 0.0001$; rare: $P = 0.013$; common: $P = 0.001$). They were also less right-handed than immature signallers for gestures with an object (Tukey test: $P = 0.036$). All elders' laterality patterns were not disproved for the remaining variable modalities. Regarding mature adult signallers they were more right-handed than adolescent signallers in RVF_R situation (Fig. 6b) as well as for rare gestures (Tukey test: RVF_R: $P = 0.037$; rare: $P = 0.004$). They were more right-handed than immature signallers for tactile gestures as well as for rare gestures, gestures directed towards medium and low affiliative partners and whatever RVF situation (Fig. 6b) and the use of communication object or not (Tukey test: tactile: $P = 0.001$; rare: $P < 0.001$; medium affiliative partner: P = 0.004; low affiliative: $P = 0.029$; RVF_R: $P = 0.004$; RVF_L: $P = 0.035$; without object: $P = 0.025$; with object: $P = 0.010$). These laterality patterns of mature adults were not disproved for the remaining variable modalities. Concerning young adult signallers they tended to use their right hand marginally more than immature signallers in RVF_L situation as well as for gestures with an object (Tukey test: RVF_L: $P = 0.071$; with object: $P = 0.095$). No statistical differences in right-hand use were evidenced between either immature and adolescent signallers or young and mature adults.

Influence of the recipient's age class. Results have not revealed any evidence of an influence of recipient's age class on signaller's right-hand use whatever the location of the recipient in the signaller's visual field during interaction (SVF).

Influence of the signaller's sex. There was no evidence of signaller's sex effect on signaller's right-hand use whatever the gesture sensory modality.

Influence of the recipient's sex. Signallers tended to be more right-handed when performing gestures towards a female than towards a male (Tukey test: $P = 0.070$).

Influence of the signaller's group (zoo). No effect of group origin on signaller's right-hand use was evidenced whatever the location of the recipient in their visual field (SVF), their position in the recipient's visual field (RVF) and the degree of gesture sharing. This was also verified for tactile and visual gestures. Nevertheless, signallers at Leipzig zoo were less right-handed than Beauval zoo subjects for auditory gestures (Tukey test: $P = 0.015$). Moreover,

signallers at Palmyre zoo tended to be moderately less right-handed than those at Beauval (resp. Leipzig) zoo when performing rare (resp. visual) gestures (Tukey test: rare: $P = 0.073$; visual: $P = 0.054$).

Discussion

The main aim of this study was to yield a detailed understanding of chimpanzees' gestural laterality by systematically evaluating the production of the most frequent gesture types of their natural repertoire. For this, we designed and applied observational and statistical procedures to assess and to compare the respective influences of factors expected to influence gestural laterality. We investigated two research questions. First, does gestural laterality differ on the population level? Second, which factors influence gestural laterality?

First, considering laterality on a continuum (McGrew & Marchant 1997), 13 of the 21 gestures considered presented a right-hand bias at the population level. Second, results of a GLMM analysis evidenced that signallers' gestural laterality was particularly influenced by characteristics of the interaction (visual fields of both signaller and recipient, emotional context), of the gestures (sensory modality, use of a communication tool, sharing degree), and signaller's hierarchical rank. More precisely, signallers used their hand ipsilateral to the recipient for tactile and visual gestures and their contralateral hand for gestures involving auditory sensory modality and a communication tool. Signallers' right-hand use was particularly pronounced for subordinates. It was also true in negative contexts for common gestures. Furthermore, elder signallers were less right-handed than than all the younger age classes.

Gestural laterality at the population level

Our findings support previous studies reporting a right-hand bias at the population level for both inter- and intra-specific communication for chimpanzees and baboons (see reviews Hopkins et al. 2012; Meguerditchian et al. 2013) indicating that laterality in gestural communication would be predominantly associated with the left hemisphere in these two species of non-human primates as in humans (see review Cochet & Byrne 2013). More precisely, several studies concerning large samples of subjects (from 33 to 227) showed a predominance of right-hand use for human-directed gestures by captive chimpanzees (FOOD BEG: Hopkins & Leavens 1998; Hopkins & Cantero 2003; Taglialatela et al. 2006; FOOD BEG

and POINTING (pooled data); Hopkins et al. 2005a; CLAPPING: Meguerditchian et al. 2012; for a category of species-typical gestures including THREAT, EXTEND ARM and HAND SLAP: Meguerditchian et al. 2010) and by captive olive baboons (FOOD BEG: Meguerditchian & Vauclair 2009; HAND SLAP: Meguerditchian & Vauclair 2006; Meguerditchian et al. 2011). Comparatively, only few studies investigated laterality in purely intra-specific communication (chimpanzees: Fletcher & Weghorst 2005; Meguerditchian et al. 2010; Hobaiter & Byrne 2013; bonobos: Chapelain 2010; olive baboons: Meguerditchian & Vauclair 2006). A predominance of right-hand use was evidenced by Meguerditchian and colleagues (2010) for 46 captive chimpanzees for a category of species-typical gestures (1241 data points) combining THREAT, EXTEND ARM and HAND SLAP and by Hobaiter and Byrne (2013) for wild chimpanzees (after pooling data across 54 subjects because of a relatively small number of data points) for a category of object-manipulation gestures combining OBJECT SHAKE and OBJECT MOVE. This predominance was also found by Meguerditchian and Vauclair (2006) for 27 baboons for HAND SLAP (442 data points from 92 social interactions).

As most studies on laterality focused on the microlevel of distinct gesture types directed towards conspecifics and/or humans (Hopkins et al. 1993; Hopkins et al. 2005b; Fletcher & Weghorst 2005; Fletcher 2006; Meguerditchian & Vauclair 2006; Chapelain 2010; Meguerditchian et al. 2012), we discuss here our findings by focusing on five gestures thereby enabling qualitative comparisons with previous reports. Our results at the population level for these five gestures are discussed according to their increasing significant p-value.

The right-hand preference we found for SLAP HAND at the population level is in accordance with Meguerditchian and Vauclair's (2006) study of baboons. Our result showing a right-hand preference at the population level for EXTEND ARM is not in agreement with Chapelain's (2010) study of bonobos who found no hand preference for ARM HELD TOWARDS THE OTHER (invitation), same gesture as EXTEND ARM but labelled differently. We found a right-hand preference at the population level for EMBRACE whereas Fletcher and Weghorst's (2005) study of chimpanzees did not. A reason of these contradictory findings might be that these authors considered a global definition of EMBRACE including not only our EMBRACE but EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, and EMBRACE HALF in addition, gestures for which we did not evidence a right-hand bias at the population level. Hopkins and colleagues (1993) have first shown in a group of 24 captive chimpanzees a right-hand bias at the population level for THROWING directed towards humans. Their finding were further supported by the Hopkins and colleagues' (2005b) study of chimpanzees which put in evidence that THROWING directed towards both humans and conspecifics (pooled data) was also right-

lateralized at the population level. Among their 89 subjects who performed THROWING at least six times, 50 were right-, 23 were left-, and 16 were ambiguously- handed. Their results are similar to our findings. We evidenced a right-hand preference at the population level for THROW OBJECT and six of the 12 subjects who performed THROW OBJECT at least six times were right-handed and one was left-handed. No bias at the population level for CLAP-HAND was detected. Nevertheless, a marginal trend was found for CLAP-HAND with a majority of subjects (7 / 8) being lateralized. This agrees with the patterns shown by Fletcher (2006) who has investigated hand preference for CLAP (an attention-getting behaviour directed towards humans) in a group of 26 captive chimpanzees. Indeed, she has reported an exclusive hand preference for a vast majority of the subjects who performed CLAP but no hand preference bias at the population level. Our result differs from Meguerditchian and colleagues' (2012) report showing a predominance of right-hand use for CLAPPING (same gesture as CLAP but labelled differently) in two colonies of captive chimpanzees totalling 94 subjects. To our knowledge, no information in the existing literature concerns any of the other eight gestures we studied that presented a right-hand bias at the population level. Our results for TOUCH BODY and TOUCH GENITAL showing no hand preference at the population level agree with Fletcher and Weghorst's (2005) study of chimpanzees for TOUCH OTHER and Chapelain's (2010) study of bonobos for TOUCH BODY and TOUCH GENITAL. In addition, we did not evidence hand preference at the population level as Chapelain (2010) did for EMBRACE LATERAL and MOVING WITH ARMS AROUND THE PARTNER (same gestures as EMBRACE HALF but labelled differently).

The influence of each factor on gestural laterality is now discussed, starting with the interactional context components, followed by gesture characteristics, and then individual social and demographic characteristics.

Factors and their mutual interactions influencing gestural laterality

Influence of interactional context on gestural laterality

Influence of the position of the recipient in the signaller's visual field during an interaction (SVF). Overall, our analyses revealed that signallers were right-handed more when the recipient was in their right visual field during an interaction (SVF_R) than in their left visual field (SVF_L) except for auditory gestures when they were more right-handed in SVF_L than in SVF_R situation. There are several explanations. First, tactile gestures require communication with physical contact with the recipient thus implying to use more likely the hand on the side of the recipient (ipsilateral hand). Visual gestures involve communication

with transmission of a visual signal and thus using the ipsilateral hand would optimize communication. Second, contrary to tactile and visual gestures, signallers used their right hand for auditory gestures more when the recipient was in their left rather than in their right visual field. In other words, the signaller used the hand on the side opposite to the recipient to perform an auditory gesture. Personal observations suggest that when a signaller plans to perform an auditory gesture, it could keep the hand on the recipient's side free to be used for a potential additional tactile or visual gesture towards the recipient.

For gestures without object, differences in right-hand use according to the position of the recipient in the signaller's visual field (SVF_R and SVF_L) could be explained as follows. As gestures without an object include 10 tactile gestures, 3 visual gestures and 3 auditory gestures, tactile and visual gestures are overrepresented in data for all gestures without an object compared to auditory gestures giving them greater weight on hand preference and this could explain our result indicating that signallers used their right hand for gestures without an object more in SVF_R than in SVF_L situation. However, no difference in right-hand use for gestures with an object (1 tactile and 4 visual gestures) between SVF_R and SVF_L situations was evidenced. This could be the consequence of a counterbalanced effect due to the fact that signallers used more the hand opposite to the recipient (contralateral hand) to communicate with an object (see below discussion of the influence of the use of communication tool in gestures). Consequently, gestures with an object would be more right-lateralized than gestures without an object when the recipient was in the signaller's left visual field.

With regard to gesture duration, long gestures involve only tactile (7) and visual (2) sensory modalities and these sensory modalities are overrepresented in short gestures (4 tactile, 5 visual and 3 auditory gestures). According to the discussion above, this would explain why signallers used their right hand to perform long and short gestures more in SVF_R than in SVF_L situation.

When taking gestures as a whole, tactile (11/21) and visual (7/21) gestures are overrepresented compared to auditory (3/21) gestures. Tactile and visual gestures thus weigh more on hand preference than auditory gestures. This could explain why signallers used their right hand more when the recipient was in their right visual field (SVF_R) than in their left visual field (SVF_L) whatever the signaller's hierarchical rank, the recipient's age class and the signaller's group.

Influence of the position of the signaller in the recipient's visual field during an interaction (RVF). Overall, our analyses showed that signallers were right-handed more when they were in the recipient's left visual field (RVF_L) than in their right visual field (RVF_R). This difference could be explained by the fact that many non-human primates display a variety of facial expressions (e.g. Bolwig 1962; Chevalier-Skolnikoff 1973). In particular, chimpanzees present a number of facial expressions in various socio-emotional contexts (e.g. review Parr et al. 2002). Facial expressions of emotions are more pronounced on the left than on the right hemiface of humans (e.g. Nicholls et al. 2002), chimpanzees (e.g. Wallez et al. 2012), rhesus macaques (e.g. Hauser 1993), and baboons (e.g. Wallez & Vauclair 2011). We hypothesize that a more pronounced recipient's facial expression (via the left visual field) would enhance the signaller's emotional state during an interaction and consequently would increase right-hand use particularly by subordinates (see below discussion about the influence of hierarchy on right-hand use).

Influence of emotional context. Common gestures were more right-lateralized when expressed in a negative context than in positive context. Brain imaging suggests that negative emotions and withdrawal motivation are associated with greater right-prefrontal activity in human brains, whereas positive emotions and approach motivation are associated with greater left-prefrontal activity (e.g. Davidson 2002, 2004; Tomarken et al. 1992). However, as mentioned by Rohlfs and Ramirez (2006), these findings must be considered with caution because of a possible confusion between emotional valence (positive-negative) and motivational direction (approach-withdrawal), as approach motivations are not always related to positive emotional valence (e.g. Carver 2001; Harmon-Jones 2003). Indeed, it has been shown that "anger" (negative in valence (e.g. Lazarus 1991; Watson et al. 1999) and which frequently elicits approach motivation (e.g. Berkowitz 1999; Darwin, 1872/1965; Plutchik 1980; Young 1943)) increased left-prefrontal brain activity resulting in humans' preferring to use their right hand in negative emotional contexts (Harmon-Jones 2004; Rohlfs & Ramirez 2006). Consequently we hypothesize that chimpanzees, a species phylogenetically close to humans, would also present this valence effect on gestural laterality and that this effect would be particularly important in terms of fitness for common gestures.

Influence of gesture characteristics on gestural laterality

Influence of gesture sensory modality. Overall, our findings indicated that signallers used their right hand more to produce visual than auditory gestures. When the recipient was in the

signaller's right visual field (SVF_R), this can be explained by the use of the ipsilateral hand for visual gestures and of the contralateral hand for auditory gestures (see above discussion about the influence of SVF on right-hand use depending on gesture sensory modality). When the recipient was in the signaller's left visual field (SVF_L), the combination of more right hand use for auditory gestures and less right-hand use for visual gestures induced absence of a significant statistical difference. Globally considering both SVF_R and SVF_L situations, signallers used thus their right hand more for visual gestures than for auditory gestures.

Overall, our findings evidenced that signallers used their right hand more for visual than for tactile gestures. In fact, signallers used their right hand more to produce visual gestures than tactile gestures in SVF_L situation but there was no statistical difference in SVF_R situation. Tactile gestures were less right-handed than visual gestures in SVF_L maybe because, although signallers preferentially use their ipsilateral hand for tactile and visual gestures, the use of this hand would be more pronounced for tactile gestures that imply physical contact than for visual gestures.

Our findings evidenced that signallers were overall more right-handed when performing tactile gestures than auditory gestures. It was the case for SVF_R situation and the contrary for SVF_L situation. These differences in right-hand use between SVF_R and SVF_L can be explained as above by the fact that signallers used more their ipsilateral hand for tactile gestures whereas they used more their contralateral hand for auditory gestures. Overall, for both SVF_R and SVF_L situations, because the LSmeans difference of 1.88 between tactile and auditory gestures in SVF_R was twice the absolute value for SVF_L (LSmeans difference = -0.89), signallers were right-handed more for tactile gestures than for auditory gestures.

Influence of the use of a communication tool. Our results showed that overall, signallers were right-handed more when performing gestures without an object than with an object. This could be because, as gestures with an object involve manipulation and communication components, these components interfere with each other. Meguerditchian and Vauclair (2006) showed that baboons' hand preference for manipulation during non-communicative tasks (tube task and a unimanual reaching task) was directed to the right less than for HAND SLAPPING (a gesture without object). We hypothesize that right-side predominance for gestures with an object is intermediate between that for manipulation (manual actions deprived of communication function) and that for gestures without an object (involving only communication components).

When the recipient was in their left visual field (SVF_L) signallers used their right hand more for gestures with an object than for gestures without an object. In other words, they used more the hand opposite the recipient (contralateral hand) to communicate with an object. An explanation would be that that they may try to prevent the recipient from grabbing the potentially coveted object (personal observation) and/or that they may keep their hand close to the recipient free to be used for further potential communication (e.g. for a PUSH).

Influence of gesture sharing degree. Communication functions are predominantly associated with left-hemisphere activity in humans (e.g. Corballis 1991; Knecht et al. 2000) and in chimpanzees (Taglialatela et al. 2006, 2008; Hopkins & Nir 2010; Meguerditchian et al. 2012) leading to predominant use of right hand. An explanation of the overall greater right-hand use by signallers for common gestures than for rare gestures could be that the former benefit by being more codified/lateralized than the latter resulting in potentially more coordination that facilitate interactions and thus social cohesion. This would be even more important for agonistic behaviour in terms of fitness because the results of agonistic interactions (for access to food, resting areas or sexual partners) influence survival and reproduction (Darwin 1859). This could be particularly pronounced for pairs of strong affiliative partners (subjects who interact frequently).

On the contrary, signallers used their right hand more for rare than for common tactile gestures. A reason might be that tactile gestures performed by few subjects were performed mainly by subordinates (68%) contrary to tactile gestures performed by many subjects (44%). Our findings showing that subordinate signallers used (resp. tended to use) their right hand for gestures more than intermediate (resp. dominant) signallers could explain this result (see below discussion about the influence of hierarchy on right-hand use).

Influence of gesture duration. Signallers used their right hand more for long gestures than for short gestures in RVF_L situation. Long gestures include 7 tactile and 2 visual gestures while short gestures include 4 tactile, 5 visual and 3 auditory gestures. Tactile gestures thus weigh more on hand preference for long gestures than for short gestures. As hypothesized above for tactile gestures in RVF_L situation, a more pronounced recipient's facial expression (via its left hemiface) could intensify the signaller's emotional states during an interaction and consequently could increase right-hand use. This might be even more important for long tactile gestures that imply close proximity for a certain time.

On the contrary, signallers used their right hand more for short gestures than for long gestures in positive emotional contexts. This could be because the type of short gestures expressed in positive and negative emotional contexts are similar, whereas this is not the case for long gestures. Long gestures expressed in positive emotional contexts include 9 gestures of which 7 are not very lateralized in direction and strength (EMBRACE, EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, HAND ON, TOUCH BODY and TOUCH GENITAL), whereas the most frequently expressed gesture (DRAG OBJECT) in negative emotional contexts is clearly right-lateralized.

Influence of social characteristics on gestural laterality

Influence of the signaller's hierarchical rank. The fact that subordinate signallers overall used more their right hand than signallers of a higher hierarchical rank (intermediate and dominant signallers) could be related to a higher level of stress as explained below. Subjects experiencing stress (e.g. competition for food, mates and territories) respond physiologically by producing high levels of glucocorticoids to optimize energy availability (Sapolsky 2002). Reports suggest that subordinate social animals would usually maintain a higher level of glucorticoïd than dominant animals (Creel 2001). Some authors report negative correlations between cortisol and primates' rank (Coe et al. 1979; Eberhart et al. 1983, 1985; Keverne et al. 1984; Manogue et al. 1975; Markham et al. 2014; Sapolsky 1982, 1990; Sapolsky et al. 1997; Shively et al. 1997; Shively 1998; Steklis et al. 1986; Yodyingyuad et al. 1985), whereas other authors report a positive correlation (Abbott et al. 1997, 1998; Ginther et al. 2001; Ziegler et al. 1995; Saltzman et al. 1994, 1996, 1998; Cavigelli et al. 2003; Muller & Wrangham 2004), and yet others found no relationships between cortisol and rank (Yodyingyuad et al. 1982; Steklis et al. 1986; McGuire et al. 1986; Martensz et al. 1987; Stavisky et al. 2001; Weingrill et al. 2004). Muller and Wrangham (2004) investigating rank effects on social stress in wild male chimpanzees found a positive correlation between male dominance rank and urinary cortisol excretion in a stable dominance hierarchy as well as a positive correlation between urinary cortisol excretion and rates of male aggression. They also found a negative correlation between urinary cortisol and food availability. Consequently, they suggested that the relationship between rank and cortisol in wild chimpanzees may be driven by metabolic stress (due to high levels of energy expenditure) more than by psychological stress. They added that psychosocial stress could play a more important role in captive populations. Markham and colleagues (2014), investigating rank effects on social stress in lactating captive chimpanzees, showed that low ranking females' faecal

glucocorticoid metabolite levels were higher than those of high ranking females. They explained that this difference could be due to psychosocial stress because subordinate females received more male aggression than dominant females. Creel and colleagues (1996) noted that artificial spatial constraints related to captivity could increase the intensity of psychosocial stress. Moreover, stress reduced captive anoles' right-hemisphere activity for aggressive movements (Deckel 1998). We hypothesize that stress produced by psychosocial factors in subordinates would reduce right-hemisphere activity (left-hand use) and so would increase right-hand use as suggested by our results for tactile gestures implying close proximity.

Influence of the recipient's hierarchical rank. We did not evidence an influence of recipients' hierarchical rank on signallers' right hand use whatever the gesture sensory modality. Differently, Baraud and colleagues (2009) reported an effect of recipient mangabeys' hierarchical rank on social laterality for approach side and positions (transversal and vertical).

Influence of kinship. We did not evidence significant kinship effect on signallers' right-hand use whatever their location with respect to the recipients' visual field during an interaction. This absence of kinship effect agrees with Hopkins and colleagues' (2005b) report investigating captive chimpanzees' hand preference for THROWING directed towards both humans and conspecifics (pooled data).

Influence of affiliation. Subordinate signallers were less right-handed for gestures towards a strong affiliative subordinate partner than towards a medium partner. We hypothesize that psychosocial stress effects (that would increase right-hand use as previously mentioned) would be less important when subordinates interact with other subordinates and this particularly during interactions involving pairs of strong affiliative partners.

Influence of individual demographic characteristics on gestural laterality

Influence of the signaller's age class. No clear effect of signaller's age on signallers' right-hand use was evidenced if all age classes are considered together. An absence of a clear signaller's age effect on laterality in the gestural communication agrees with results of the following studies: for chimpanzees for THROWING directed towards both humans and conspecifics (pooled data) (Hopkins et al. 2005b); for baboons for human-directed FOOD BEG (Meguerditchian & Vauclair 2009). However, the following three age groups emerged from our analysis: immatures and adolescents, young and mature adults, and elders. In fact, elder

signallers were less right-handed than adolescent, young and mature adult signallers and mature adult signallers were more right-handed than adolescent and immature signallers. This decrease in right-hand use by elder subjects has already been documented by Kalisch and colleagues (2006) for humans. A reason might be that physical limitations and lower activity (Hughes et al. 1997; Schut 1998; Ranganathan et al. 2001) associated with aging could decrease the practice-based performance of the right hand that would thus converge towards the performance of the left hand. We can assume that lower sociality observed in our elder subjects could also produce a shift towards ambidexterity with aging in chimpanzees. To our knowledge, this is the first evidence of a possible senescence effect on manual laterality of non-human primates.

Considering the two age groups: immatures and adolescents, and young and mature adults, a trend towards an increase of right-hand use with age emerged. This agrees with reports indicating that right direction in hand preference increases with age: for wild chimpanzees for 20 gesture types (pooled data) (Hobaiter & Byrne 2013) and for captive chimpanzees for human-directed FOOD BEG and POINTING (pooled data) (Hopkins & Leavens 1998); for baboons for HAND SLAP directed towards both humans and conspecifics (pooled data) (Meguerditchian & Vauclair 2006).

Influence of the signaller's sex. We found no evidence of signaller's sex on signallers' right-hand use whatever the gesture sensory modality. This absence of signaller's sex effect supports previous reports investigating manual laterality in the gestural communication (e.g.in captive chimpanzees for human-directed FOOD BEG (Meguerditchian et al. 2010), for THROWING directed towards both humans and conspecifics, (pooled data) (Hopkins et al. 2005b), and for a category of species-typical gestures including THREAT, EXTENDED ARM and HAND SLAP, directed towards both humans and conspecifics (pooled data for the sex effect analysis), Meguerditchian et al. 2010); in captive baboons for human-directed FOOD BEG, (Meguerditchian & Vauclair 2009) and for HAND SLAP directed towards both humans and conspecifics, (pooled data) (Meguerditchian & Vauclair 2006)).

Influence of the recipient's sex. Signallers tended to be right-handed more for gestures towards a female than towards a male. This could be explained by the fact that most signallers interacting with females were males using common gestures. As previously hypothesized, common gestures could be more strongly codified/lateralized than rare gestures to facilitate

social interactions. This would be particularly beneficial in terms of fitness (e.g. reproductive success) concerning males' gestures directed towards females.

Influence of the signaller's group (zoo). Overall, we did not evidence a group effect on signaller's right-hand use. This absence of group effect on gestural laterality agrees with reports for captive chimpanzees (for human-directed CLAPPING (Meguerditchian et al. 2012) and for THROWING directed towards both humans and conspecifics (pooled data) (Hopkins et al. 2005b)) and for captive baboons (HAND SLAP directed towards both humans and conspecifics (pooled data) (Meguerditchian et al. 2011)).

However, we evidenced a group effect as Leipzig signallers were less right-handed than Beauval signallers for auditory gestures. Laterality of auditory gestures could have been influenced by heredity. Subjects in each group are relatively closely related. Groups might differ genetically from one another. Lonsdorf and Hopkins (2005) suggested that genetic factors and/or social learning could explain variation in laterality patterns of tool use (in non-communication actions) between groups (as shown for handedness in humans (e.g. Fagard (2013)). Moreover, Taglialatela and colleagues' (2012) study of chimpanzees supports the hypothesis that social learning participates in the acquisition and use of attention-getting vocalizations. This might also be the case in gestural communication as we reported for auditory gestures.

The main aim of this study was to improve our understanding of chimpanzees' social laterality in the most frequent gestures of their natural communication repertoire and to evaluate the influence of factors expected to modulate hand-preference. To conclude, our results convincingly show that our chimpanzee subjects were right-handed at the population level for the majority of intraspecific gestures considered. Laterality was influenced by several factors and their mutual intertwinement: interactional context (visual fields of both signaller and recipient as well as emotional context), gesture characteristics (sensory modality, use of a communication tool, and sharing degree) and by certain socio-demographic components in particular signaller's hierarchical rank. Signallers used their hand ipsilateral to the recipient for tactile and visual gestures and their contralateral hand for gestures involving the auditory sensory modality or a communication tool. Moreover, signallers' right-hand use was more pronounced in negative contexts for common gestures as well as for subordinates performing tactile gestures. Overall, our results support the Ghirlanda and colleagues' (2009) model predicting that population-level bias could be explained by an evolutionnary stable

strategy based on intraspecific interactions. Our results also support the origin of human language theory postulating that laterality in gestural communication represents a precursor of the left-hemispheric lateralization of language. Our findings emphasize the need to deeply investigate social laterality to understand better relationships between cerebral lateralization and population-level laterality. In an evolutionary perspective, it would be especially important that further studies consider socioecologically relevant contexts, namely contexts in which subjects interact with conspecifics in suitable environments: in the wild and/or in favourable captive conditions (when naturalization of enclosures is optimal and social groups include many subjects). Furthermore, a comparative approach using standardized methodologies, including species varying in their degree of sociality, and taking into account multiple potentially influential factors is necessary.

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Table notes

Table 1. F: Female; M: Male

Table 2. Gestures are regrouped by sensory modality (3 auditory, 11 tactile and 7 visual gestures) and presented by alphabetic order. Gestures marked with * are followed by descriptions inspired from the mentioned reference(s), except for EXTEND HAND, they are labelled differently because details based on personal observations have been added.

Table 3. Gestures are regrouped by sensory modality and classified by increasing HI values. *N*: number of subjects who performed at least 6 times each gesture; Data points analysed: number of data points associated with the N analysed subjects; Non-lat.: numbers of non-lateralized subjects; B test Lat. vs. Non-lat.: p-value of the binomial test on the numbers of lateralized versus non-lateralized subjects; LH: number of left-handed subjects; RH: number of right-handed subjects; B test LH vs. RH: p-value of the binomial test on the numbers of left-handed versus right-handed subjects; -: insufficient number of lateralized subjects for testing; Mean HI: Mean Handedness Index score of N analysed subjects, the sign indicates the direction of the gestural 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 only performed when normality of HI values is not verified; Mean ABSHI: Mean Absolute value of Handedness Index score of N analysed subjects. Significant results are in bold.

Table 4. L: Left; R: Right; F: Female; M: Male

Table 5. χ^2: value of type II Wald chi-square; Df: Degree of freedom; *P*: p-value of type II Wald chi-square. Significant results are in bold.

Table 6. L: Left; R: Right; A>B: means "signallers used their right hand more when A than when B"; X: statistical evidence

Table A1. HI: Gestures are regrouped by sensory modality (3 auditory, 11 tactile and 7 visual gestures) and presented by alphabetic order. Handedness Index; ABSHI: Mean Absolute

value of Handedness Index; rs: Spearman's rho; *P*: Spearman's p-value; *N*: number of subjects who performed the considered gesture at least 6 times each. Significant results are in bold.

Table A2. L: Left; R: Right; F: Female; M: Male; Imm.: Immature; Ado.: Adolescent; Y.adu.: Young adult; M.adu.: Mature adult; Eld.: Elder; estimate: difference between LSmeans SE: Standard Error of the difference; z.ratio: ratio of the estimate to its standard error**;** *P*: Tukey's p-value. Significant results are in bold.

Table 1. Individual characteristics of the study sample.

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

Table 2. Gestural repertoire and detailed description

Gesture	Description	Reference(s)
CLAP HAND *	One open hand (more often the one in the upper position) strikes against the other hand	Call & Tomasello (2007)
SLAP FOOT *	Subject hits ground/wall/object with the sole or heel of one foot	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 arm of signaller is stretched and raised up to about head level with palm facing downwards or placed lightly on the recipient's body	Roth (1995)
EMBRACE HALF	Subject puts one arm around another subject while walking	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)
HAND ON	The palm of one hand is placed on the head of another subject and stays there >2 sec	Pika et al. (2003, 2005)
HIT WITH OBJECT *	Subject clubs another subject with object (e.g. branch) held in one hand	Nishida et al. (1999, 2010)
KICK *	Any sort of contact made with the sole/heel or fingers of one foot with another subject, without appreciable force, but the actual contact is more forceful than a simple laying of foot on another's body	Pollick & de Waal (2007)
PUNCH *	Any sort of contact made with fist/wrist or fingers of one hand with another subject, without appreciable force, but the actual contact is more forceful than a simple laying of the hand on another's body	Pollick & de Waal (2007)
PUSH	Gentle pressure applied against another subject with one hand or arm	Call & Tomasello 2007
TOUCH BODY *	Gentle and brief (<5 sec) contact of the recipient's body (except genitals) with one hand or arm	Pika et al. (2003, 2005)
TOUCH GENITAL *	Gentle and brief (<5 sec) contact of the recipient's genitals with the flat of one hand	Pika et al. (2003, 2005)
ATTEMPT TO REACH *	Subject briefly extends hand (with fingers slightly flexed with palm up or down) towards another subject, as an attempt to touch/catch it	Pika et al. (2003, 2005)
DRAG OBJECT	Subject pulls an object (e.g. branch)on the ground with one hand towards another subject	Nishida et al. (1999, 2010)
EXTEND HAND *	Subject outstretches one hand or arm (wrist and/or fingers extended with palm up or down) towards another subject; hand or arm remains stationary	Goodall (1989)
PUT OBJECT ON HEAD/BACK *	Subject places an object (e.g. branch) on its head/back with one hand	Nishida et al. (2010)
RAISE ARM	Subject lifts one out-stretched arm (all or only forearm) overhead in a quick jerky movement with fingers slightly flexed	Plooij (1984)
SHAKE OBJECT *	An object (e.g. branch) is moved back and forth with quick jerky movements of one arm, slightly or vigorously, while the subject is sitting or standing	Kano (1992, 1998)
THROW OBJECT *	Subject sends an object (e.g. branch) through the air with one hand towards another subject	Hohmann & Fruth (2003a, b)

Table 3. Characteristics, descriptive statistics and analyses of each gesture

Gesture	Sensory modality	Communication tool	Duration	Sharing degree	*N*	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
CLAP HAND	Auditory	–	Short	Low	8	177	1	0.070	4	3	1	-0.151	**0.009**	W=16.5 , p=0.889	0.836
SLAP HAND	Auditory	–	Short	High	33	2850	16	1	0	17	**0**	0.391	0.867	t=0.391 , **p<0.0001**	0.400
SLAP FOOT	Auditory	–	Short	High	21	1412	10	1	0	11	**0.001**	0.468	**0.012**	W=223.5 , **p=0.0002**	0.513
TOUCH GENITAL	Tactile	–	Long	High	29	692	25	**0.0001**	2	2	-	-0.079	0.299	t=-0.079 , p=0.237	0.261
HAND ON	Tactile	–	Long	High	30	581	23	**0.005**	5	2	0.453	-0.052	0.474	t=-0.052 , p=0.472	0.281
EMBRACE LATERAL	Tactile	–	Long	High	29	1339	25	**0.0001**	2	2	-	0.016	**0.044**	W=219 , p=0.478	0.236
EMBRACE VENTRAL/DORSAL	Tactile	–	Long	Low	13	686	10	0.092	1	2	-	0.056	0.925	t=0.077 , p=0.107	0.224
TOUCH BODY	Tactile	–	Long	High	39	4203	35	**0**	1	3	-	0.060	**0.011**	W=456.5 , p=0.215	0.149
EMBRACE HALF	Tactile	–	Long	Low	12	623	11	**0.006**	0	1	-	0.064	0.353	t=0.064 , p=0.264	0.154
PUSH	Tactile	–	Short	High	24	464	20	**0.002**	0	4	-	0.101	0.618	t=0.101 , p=0.113	0.260
EMBRACE	Tactile	–	Long	High	31	771	28	**0**	1	2	-	0.188	0.759	t=0.188 , **p=0.0008**	0.276
KICK	Tactile	–	Short	Low	8	95	8	**0.008**	0	0	-	0.291	0.558	t=0.291 , **p=0.009**	0.291
PUNCH	Tactile	–	Short	High	34	1654	18	0.864	0	16	**0**	0.317	0.858	t=0.317 , **p<0.0001**	0.348
HIT WITH OBJECT	Tactile	Yes	Short	Low	12	248	7	0.774	0	5	-	0.466	0.745	t=0.466 , **p=0.0004**	0.491
ATTEMPT TO REACH	Visual	–	Short	High	31	831	23	**0.011**	1	7	0.070	0.202	0.973	t=0.202 , **p=0.003**	0.325
DRAG OBJECT	Visual	Yes	Long	Low	13	488	11	**0.023**	0	2	-	0.257	0.845	t=0.256 , **p=0.0005**	0.282
PUT OBJECT ON HEAD/BACK	Visual	Yes	Short	Low	11	386	6	1	0	5	-	0.302	0.591	t=0.302 , **p=0.024**	0.398
SHAKE OBJECT	Visual	Yes	Short	High	38	5095	18	0.871	1	19	**0**	0.314	0.340	t=0.314 , **p<0.0001**	0.352
EXTEND HAND	Visual	–	Long	High	37	1226	21	0.511	0	16	**0**	0.381	0.860	t=0.381 , **p<0.0001**	0.394
THROW OBJECT	Visual	Yes	Short	Low	12	347	5	0.774	1	6	0.125	0.411	0.056	t=0.411 , **p=0.021**	0.598
RAISE ARM	Visual	–	Short	High	25	856	11	0.690	0	14	**0.0001**	0.471	**0.017**	W=311 , **p<0.0001**	0.543

Table 4. Generalized linear mixed model with dependent, fixed and random variables, their type and associated levels

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

Table 5. Analysis of deviance table (Type II Wald chi-square tests)

Fixed variables and associated interactions	χ^2	Df	*P*
Kinship	0.087	2	0.958
Position of signaller in Recipient's Visual Field during an interaction (RVF)	75.037	1	<2.2e-16
Emotional context	16.245	1	5.565e-5
Recipient's age class	3.466	4	0.483
Position of recipient in Signaller's Visual Field during an interaction (SVF)	2515.340	1	<2.2e-16
Recipient's sex	3.285	1	0.070
Sharing degree of gesture	7.818	1	0.005
Signaller's hierarchical rank	3.791	2	0.150
Affiliation	6.038	2	0.049
Signaller's age class	6.079	4	0.193
Zoo	1.823	2	0.402
Gesture sensory modality	121.041	2	<2.2e-16
Signaller's sex	0.203	1	0.653
Recipient's hierarchical rank	1.235	2	0.539
Gesture duration	17.971	1	2.242e-5
Use of communication tool	2.769	1	0.096
Kinship × RVF	16.216	2	**3.012e-4**
Kinship × Emotional context	8.425	2	**0.015**
Recipient's age class × SVF	15.801	4	**0.003**
Sharing degree of gesture × Signaller's hierarchical rank	8.320	2	**0.016**
Sharing degree of gesture × Affiliation	9.374	2	**0.009**
Sharing degree of gesture × Signaller's age class	44.502	4	**5.046e-9**
Emotional context × Sharing degree of gesture	8.957	1	**0.003**
Sharing degree of gesture × Zoo	17.516	2	**1.572e-4**
Sharing degree of gesture × Gesture sensory modality	76.143	2	**<2.2e-16**
Signaller's hierarchical rank × Gesture sensory modality	10.455	4	**0.033**
Gesture sensory modality × Signaller's sex	11.864	2	**0.003**
Signaller's age class × Gesture sensory modality	30.663	8	**1.613e-4**
SVF × Gesture sensory modality	532.771	2	**<2.2e-16**
RVF × Gesture sensory modality	75.677	2	**<2.2e-16**
Emotional context × Gesture sensory modality	6.494	2	**0.039**
Gesture sensory modality × Recipient's hierarchical rank	11.752	4	**0.019**
Zoo × Gesture sensory modality	68.903	4	**3.869e-14**
Signaller's sex × Gesture duration	11.886	1	**5.657e-4**
SVF × Gesture duration	12.678	1	**3.701e-4**
RVF × Gesture duration	32.419	1	**1.243e-8**
Emotional context × Gesture duration	5.538	1	**0.019**
Signaller's age class × Use of communication tool	33.973	4	**7.549e-7**
SVF × Use of communication tool	403.511	1	**<2.2e-16**
RVF × Use of communication tool	22.960	1	**1.654e-6**
Emotional context × Use of communication tool	3.798	1	0.051
RVF × Signaller's hierarchical rank	4.776	2	0.092
RVF × Signaller's age class	21.411	4	**2.624e-4**
RVF × Zoo	9.714	2	**0.008**
SVF × Signaller's hierarchical rank	22.186	2	**1.522e-5**
SVF × Zoo	32.311	2	**9.635e-8**
Affiliation × Signaller's age class	26.942	8	**7.236e-4**
Signaller's hierarchical rank × Affiliation	11.130	4	**0.025**

Table 6. Generalized linear mixed model: summary of results

		Influence of interactional context					
		SVF		*RVF*		*Emotional context*	
		SVF_R>SFV_L	SVF_R<SFV_L	RVF_L>RFV_R	RVF_L<RFV_R	N>P	N<P
Position of recipient in Signaller's Visual Field during interaction (SVF)	SVF_R						
	SVF_L						
Position of signaller in Recipient's Visual Field during interaction (RVF)	RVF_R						
	RVF_L						
Emotional context	Positive (P)						
	Negative (N)						
Gestures	Tactile (T)	X		X			
	Visual (V)	X					
	Auditory (A)		X	X			
	With object			X			
	Without object	X		X			
	Short (Sh)	X		X			
	Long (Lo)	X		X			
	Rare (Ra)						
	Common (C)					X	
Kinship	Parent-infant			X			
	Siblings						
	Unrelated			X			
Signaller's hierarchical rank	Subordinate (Sub)	X		X			
	Intermediate (Int)	X		X			
	Dominant (Dom)	X		X			
Recipient's hierarchical rank	Subordinate (Sub)						
	Intermediate (Int)						
	Dominant (Dom)						
Affiliation	Strong (St)						
	Medium (Me)						
	Low						
Signaller's age class	Immature (Im)			X			
	Adolescent (Ad)			X			
	Young Adult (YA)			X			
	Mature Adult (MA)						
	Elder (E)						
Signaller's sex	Male (M)						
	Female (F)						
Recipient's age class	Immature (Im)	X					
	Adolescent (Ad)	X					
	Young Adult (YA)	X					
	Mature Adult (MA)	X					
	Elder (E)	X					
Zoo	La Palmyre	X		X			
	Beauval (B)	X		X			
	Leipzig (Le)	X		X			

Table 6. continued

		Influence of gesture characteristics											
		Sensory modality						*Communication tool*		*Duration*		*Sharing degree*	
		A>V	A<V	A>T	A<T	T>V	T<V	Without >With object	Without< With object	Sh>Lo	Sh<Lo	C>Ra	C<Ra
Position of recipient in Signaller's Visual Field during interaction (SVF)	SVF_R		X		X			X					
	SVF_L			X			X		X		X		
Position of signaller in Recipient's Visual Field during interaction (RVF)	RVF_R		X				X	X					
	RVF_L				X			X					
Emotional context	Positive (P)		X				X	X		X			
	Negative (N)		X		X			X				X	
Gestures	Tactile (T)												X
	Visual (V)												
	Auditory (A)											X	
	With object												
	Without object												
	Short (Sh)												
	Long (Lo)												
	Rare (Ra)		X		X								
	Common (C)			X			X						
Kinship	Parent-infant												
	Siblings												
	Unrelated												
Signaller's hierarchical rank	Subordinate (Sub)												
	Intermediate (Int)		X										
	Dominant (Dom)		X		X		X					X	
Recipient's hierarchical rank	Subordinate (Sub)		X		X								
	Intermediate (Int)		X										
	Dominant (Dom)		X		X		X						
Affiliation	Strong (St)											X	
	Medium (Me)												
	Low												
Signaller's age class	Immature (Im)		X				X	X				X	
	Adolescent (Ad)							X					
	Young Adult (YA)		X		X								
	Mature Adult (MA)				X								
	Elder (E)		X				X	X					
Recipient's age class	Immature (Im)												
	Adolescent (Ad)												
	Young Adult (YA)												
	Mature Adult (MA)												
	Elder (E)												
Signaller's sex	Male (M)		X		X								
	Female (F)		X				X						
Zoo	La Palmyre											X	
	Beauval (B)		X										
	Leipzig (Le)		X		X		X						

Table 6. continued

		Influence of individual social characteristics			**Influence of individual demographic characteristics**						
		Signaller's hierarchical rank		*Affiliation*	*Signaller's age class*						*Signaller's group (zoo)*
		Sub>Int	Sub>Dom	Me>St	E<MA	E<YA	E<Ad	E<Im	MA>Ad	MA>Im	B>Le
Position of recipient in Signaller's Visual Field during interaction (SVF)	SVF_R		X								
	SVF_L	X									
Position of signaller in Recipient's Visual Field during interaction (RVF)	RVF_R				X	X	X		X	X	
	RVF_L	X			X	X	X			X	
Emotional context	Positive (P)										
	Negative (N)										
Gestures	Tactile (T)	X			X	X	X			X	
	Visual (V)				X						
	Auditory (A)				X		X				X
	With object				X	X	X	X		X	
	Without object				X					X	
	Short (Sh)										
	Long (Lo)										
	Rare (Ra)	X	X		X	X	X		X	X	
	Common (C)					X	X				
Kinship	Parent-infant										
	Siblings										
	Unrelated										
Signaller's hierarchical rank	Subordinate (Sub)			X							
	Intermediate (Int)										
	Dominant (Dom)										
Recipient's hierarchical rank	Subordinate (Sub)										
	Intermediate (Int)										
	Dominant (Dom)										
Affiliation	Strong (St)				X		X				
	Medium (Me)	X	X		X	X	X			X	
	Low				X	X				X	
Signaller's age class	Immature (Im)										
	Adolescent (Ad)										
	Young Adult (YA)										
	Mature Adult (MA)										
	Elder (E)										
Recipient's age class	Immature (Im)										
	Adolescent (Ad)										
	Young Adult (YA)										
	Mature Adult (MA)										
	Elder (E)										
Signaller's sex	Male (M)										
	Female (F)										
Zoo	La Palmyre										
	Beauval (B)										
	Leipzig (Le)										

Table A1. Effect of the number of data points for each subject on laterality for each gesture

Gesture	Spearman correlation test between number of data points and HI values			Spearman correlation test between number of data points and ABSHI values		
CLAP HAND	rs = -0.570	*P* = 0.140	*N* = 8	rs = 0.265	*P* = 0.527	*N* = 8
SLAP FOOT	rs = 0.139	*P* = 0.548	*N* = 21	rs = 0.033	*P* = 0.888	*N* = 21
SLAP HAND	rs = 0.033	*P* = 0.854	*N* = 33	rs = 0.018	*P* = 0.922	*N* = 33
EMBRACE	rs = -0.254	*P* = 0.169	*N* = 31	rs = -0.233	*P* = 0.206	*N* = 31
EMBRACE HALF	rs = 0.102	*P* = 0.752	*N* = 12	rs = -0.092	*P* = 0.775	*N* = 12
EMBRACE LATERAL	rs = 0.097	*P* = 0.617	*N* = 29	rs = -0.261	*P* = 0.172	*N* = 29
EMBRACE VENTRAL/DORSAL	rs = 0.044	*P* = 0.887	*N* = 13	rs = -0.009	*P* = 0.977	*N* = 13
HAND ON	rs = 0.008	*P* = 0.967	*N* = 30	rs = -0.129	*P* = 0.499	*N* = 30
HIT WITH OBJECT	rs = -0.474	*P* = 0.119	*N* = 12	rs = -0.256	*P* = 0.422	*N* = 12
KICK	rs = -0.642	*P* = 0.086	*N* = 8	rs = -0.642	*P* = 0.086	*N* = 8
PUNCH	rs = 0.043	*P* = 0.810	*N* = 34	rs = 0	*P* = 0.998	*N* = 34
PUSH	rs = 0.425	***P* = 0.039**	*N* = 24	rs = 0.452	***P* = 0.026**	*N* = 24
TOUCH BODY	rs = -0.213	*P* = 0.193	*N* = 39	rs = -0.469	***P* = 0.003**	*N* = 39
TOUCH GENITAL	rs = 0.057	*P* = 0.768	*N* = 29	rs = -0.258	*P* = 0.177	*N* = 29
DRAG OBJECT	rs = 0.017	*P* = 0.955	*N* = 13	rs = -0.097	*P* = 0.753	*N* = 13
EXTEND HAND	rs = -0.064	*P* = 0.705	*N* = 37	rs = -0.074	*P* = 0.666	*N* = 37
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
RAISE ARM	rs = 0.093	*P* = 0.660	*N* = 25	rs = -0.061	*P* = 0.773	*N* = 25
ATTEMPT TO REACH	rs = 0.160	*P* = 0.389	*N* = 31	rs = -0.101	*P* = 0.588	*N* = 31

Table A2. Results of post-hoc multiple comparisons tests

Recipient's sex						
contrast			estimate	SE	z.ratio	*P*
F	-	M	0.117	0.065	1.812	0.070
Kinship × RVF						
contrast			estimate	SE	z.ratio	*P*
Parent-infant,R	-	Siblings,R	-0.253	0.122	-2.075	0.301
Parent-infant,R	-	Unrelated,R	-0.243	0.100	-2.428	0.147
Parent-infant,R	-	Parent-infant,L	-0.795	0.115	-6.939	< **0.0001**
Siblings,R	-	Unrelated,R	0.010	0.091	0.113	1.000
Siblings,R	-	Siblings,L	-0.237	0.110	-2.160	0.257
Unrelated,R	-	Unrelated,L	-0.503	0.071	-7.107	< **0.0001**
Parent-infant,L	-	Siblings,L	0.305	0.127	2.390	0.160
Parent-infant,L	-	Unrelated,L	0.049	0.105	0.469	0.997
Siblings,L	-	Unrelated,L	-0.256	0.093	-2.738	0.068
Kinship × Emotion						
contrast			estimate	SE	z.ratio	*P*
Parent-infant,N	-	Siblings,N	0.054	0.171	0.313	1.000
Parent-infant,N	-	Unrelated,N	-0.237	0.158	-1.499	0.665
Parent-infant,N	-	Parent-infant.,P	0.233	0.253	0.923	0.941
Siblings,N	-	Unrelated,N	-0.290	0.118	-2.467	0.134
Siblings,N	-	Siblings,P	0.177	0.220	0.807	0.966
Unrelated,N	-	Unrelated,P	0.513	0.205	2.501	0.124
Parent-infant,P	-	Siblings,P	-0.002	0.096	-0.026	1.000
Parent-infant,P	-	Unrelated,P	0.043	0.070	0.606	0.991
Siblings,P	-	Unrelated,P	0.045	0.075	0.604	0.991
Recipient's age class × SVF						
contrast			estimate	SE	z.ratio	*P*
Eld.,R	-	Ado.,R	-0.302	0.109	-2.778	0.144
Eld.,R	-	Imm.,R	-0.214	0.111	-1.931	0.648
Eld.,R	-	M.adu.,R	-0.009	0.107	-0.086	1.000
Eld.,R	-	Y.adu.,R	-0.274	0.117	-2.353	0.355
Eld.,R	-	Eld.,L	0.972	0.118	8.269	< **0.0001**
Ado.,R	-	Imm.,R	0.087	0.103	0.846	0.998
Ado.,R	-	M.adu.,R	0.292	0.102	2.872	0.114
Ado.,R	-	Y.adu.,R	0.027	0.091	0.298	1.000
Ado.,R	-	Ado.,L	1.270	0.099	12.845	< **0.0001**
Imm.,R	-	M.adu.,R	0.205	0.114	1.799	0.736
Imm.,R	-	Y.adu.,R	-0.060	0.105	-0.570	1.000
Imm.,R	-	Imm.,L	1.181	0.078	15.127	< **0.0001**
M.adu.,R	-	Y.adu.,R	-0.265	0.102	-2.599	0.218
M.adu.,R	-	M.adu.,L	0.870	0.091	9.608	< **0.0001**
Y.adu.,R	-	Y.adu.,L	1.209	0.097	12.468	< **0.0001**
Eld.,L	-	Ado.,L	-0.004	0.102	-0.037	1.000
Eld.,L	-	Imm.,L	-0.006	0.106	-0.053	1.000
Eld.,L	-	M.adu.,L	-0.111	0.103	-1.076	0.987
Eld.,L	-	Y.adu.,L	-0.037	0.110	-0.339	1.000
Ado.,L	-	Imm.,L	-0.002	0.097	-0.019	1.000
Ado.,L	-	M.adu.,L	-0.107	0.096	-1.110	0.984
Ado.,L	-	Y.adu.,L	-0.034	0.082	-0.407	1.000
Imm.,L	-	M.adu.,L	-0.105	0.112	-0.938	0.995
Imm.,L	-	Y.adu.,L	-0.032	0.100	-0.318	1.000
M.adu.,L	-	Y.adu.,L	0.073	0.097	0.758	0.999

Table A2. continued

Sharing degree × Signaller's hierarchical rank						
contrast			estimate	SE	z.ratio	*P*
Low,Dominant	-	High,Dominant	-0.453	0.147	-3.086	**0.025**
Low,Dominant	-	Low,Intermediate	-0.048	0.270	-0.179	1.000
Low,Dominant	-	Low,Subordinate	-0.997	0.341	-2.928	**0.040**
High,Dominant	-	High,Intermediate	-0.094	0.185	-0.509	0.996
High,Dominant	-	High,Subordinate	-0.390	0.240	-1.626	0.581
Low,Intermediate	-	High,Intermediate	-0.499	0.202	-2.470	0.133
Low,Intermediate	-	Low,Subordinate	-0.949	0.295	-3.212	**0.017**
High,Intermediate	-	High,Subordinate	-0.296	0.196	-1.504	0.662
Low,Subordinate	-	High,Subordinate	0.155	0.214	0.721	0.979
Sharing degree × Affiliation						
contrast			estimate	SE	z.ratio	*P*
Low,Strong	-	High,Strong	-0.471	0.162	-2.904	**0.043**
Low,Strong	-	Low,Low	-0.238	0.153	-1.554	0.629
Low,Strong	-	Low,Medium	-0.425	0.172	-2.475	0.132
High,Strong	-	High,Low	-0.114	0.084	-1.361	0.751
High,Strong	-	High,Medium	0.065	0.091	0.722	0.979
Low,Low	-	High,Low	-0.347	0.132	-2.627	0.091
Low,Low	-	Low,Medium	-0.187	0.172	-1.088	0.887
High,Low	-	High,Medium	0.180	0.070	2.565	0.106
Low,Medium	-	High,Medium	0.020	0.182	0.109	1.000
Sharing degree × Signaller's age class						
contrast			estimate	SE	z.ratio	*P*
Low,Eld.	-	High,Eld.	-0.924	0.345	-2.674	0.184
Low,Eld.	-	Low,Ado.	-1.459	0.408	-3.579	**0.013**
Low,Eld.	-	Low,Imm.	-0.562	0.420	-1.340	0.944
Low,Eld.	-	Low,M.adu.	-2.735	0.454	-6.019	< **0.0001**
Low,Eld.	-	Low,Y.adu.	-1.723	0.446	-3.864	**0.004**
High,Eld.	-	High,Ado.	-0.938	0.226	-4.149	**0.001**
High,Eld.	-	High,Imm.	-0.560	0.237	-2.360	0.350
High,Eld.	-	High,M.adu.	-0.729	0.252	-2.891	0.108
High,Eld.	-	High,Y.adu.	-0.963	0.262	-3.678	**0.009**
Low,Ado.	-	High,Ado.	-0.403	0.197	-2.044	0.567
Low,Ado.	-	Low,Imm.	0.896	0.348	2.577	0.229
Low,Ado.	-	Low,M.adu.	-1.276	0.327	-3.906	**0.004**
Low,Ado.	-	Low,Y.adu.	-0.265	0.286	-0.927	0.996
High,Ado.	-	High,Imm.	0.378	0.252	1.499	0.893
High,Ado.	-	High,M.adu.	0.209	0.228	0.917	0.996
High,Ado.	-	High,Y.adu.	-0.025	0.211	-0.118	1.000
Low,Imm.	-	High,Imm.	-0.921	0.182	-5.053	< **0.0001**
Low,Imm.	-	Low,M.adu.	-2.172	0.408	-5.329	< **0.0001**
Low,Imm.	-	Low,Y.adu.	-1.161	0.399	-2.913	0.102
High,Imm.	-	High,M.adu.	-0.169	0.287	-0.589	1.000
High,Imm.	-	High,Y.adu.	-0.403	0.274	-1.470	0.904
Low,M.adu.	-	High,M.adu.	1.082	0.257	4.215	**0.001**
Low,M.adu.	-	Low,Y.adu.	1.011	0.352	2.874	0.113
High,M.adu.	-	High,Y.adu.	-0.234	0.238	-0.986	0.993
Low,Y.adu.	-	High,Y.adu.	-0.163	0.228	-0.715	0.999

Table A2. continued

Emotion × Sharing degree						
contrast			estimate	SE	z.ratio	*P*
N,Low	-	P,Low	-0.030	0.249	-0.122	0.999
N,Low	-	N,High	-0.604	0.210	-2.878	**0.021**
P,Low	-	P,High	0.072	0.126	0.573	0.940
N,High	-	P,High	0.646	0.221	2.923	**0.018**
Sharing degree × Zoo						
contrast			estimate	SE	z.ratio	*P*
Low,Leipzig	-	High,Leipzig	-0.052	0.128	-0.407	0.999
Low,Leipzig	-	Low,Beauval	-0.182	0.216	-0.844	0.959
Low,Leipzig	-	Low,Palmyre	0.426	0.196	2.176	0.249
High,Leipzig	-	High,Beauval	-0.290	0.152	-1.914	0.394
High,Leipzig	-	High,Palmyre	-0.107	0.150	-0.717	0.980
Low,Beauval	-	High,Beauval	-0.160	0.176	-0.910	0.944
Low,Beauval	-	Low,Palmyre	0.608	0.224	2.712	0.073
High,Beauval	-	High,Palmyre	0.183	0.168	1.090	0.886
Low,Palmyre	-	High,Palmyre	-0.585	0.167	-3.506	**0.006**
Sharing degree × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
Low,Auditory	-	High,Auditory	-1.458	0.211	-6.919	< **0.0001**
Low,Auditory	-	Low,Tactile	-1.439	0.224	-6.411	< **0.0001**
Low,Auditory	-	Low,Visual	-1.691	0.234	-7.217	< **0.0001**
High,Auditory	-	High,Tactile	0.450	0.105	4.298	**0.0003**
High,Auditory	-	High,Visual	-0.004	0.109	-0.037	1.000
Low,Tactile	-	High,Tactile	0.431	0.148	2.914	**0.042**
Low,Tactile	-	Low,Visual	-0.252	0.139	-1.813	0.457
High,Tactile	-	High,Visual	-0.454	0.095	-4.765	< **0.0001**
Low,Visual	-	High,Visual	0.229	0.145	1.582	0.611
Signaller's hierarchical rank × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
Dominant,Auditory	-	Intermediate,Auditory	-0.370	0.266	-1.392	0.901
Dominant,Auditory	-	Subordinate,Auditory	-0.902	0.354	-2.547	0.210
Dominant,Auditory	-	Dominant,Tactile	-0.618	0.165	-3.748	**0.006**
Dominant,Auditory	-	Dominant,Visual	-1.231	0.167	-7.386	< **0.0001**
Intermediate,Auditory	-	Subordinate,Auditory	-0.532	0.291	-1.824	0.666
Intermediate,Auditory	-	Intermediate,Tactile	-0.305	0.192	-1.589	0.811
Intermediate,Auditory	-	Intermediate,Visual	-0.647	0.202	-3.204	**0.037**
Subordinate,Auditory	-	Subordinate,Tactile	-0.560	0.238	-2.348	0.314
Subordinate,Auditory	-	Subordinate,Visual	-0.665	0.241	-2.758	0.128
Dominant,Tactile	-	Intermediate,Tactile	-0.058	0.218	-0.265	1.000
Dominant,Tactile	-	Subordinate,Tactile	-0.844	0.281	-2.999	0.068
Dominant,Tactile	-	Dominant,Visual	-0.614	0.124	-4.938	< **0.0001**
Intermediate,Tactile	-	Subordinate,Tactile	-0.786	0.232	-3.384	**0.021**
Intermediate,Tactile	-	Intermediate,Visual	-0.342	0.149	-2.288	0.349
Subordinate,Tactile	-	Subordinate,Visual	-0.105	0.173	-0.608	1.000
Dominant,Visual	-	Intermediate,Visual	0.214	0.223	0.960	0.989
Dominant,Visual	-	Subordinate,Visual	-0.335	0.279	-1.201	0.957
Intermediate,Visual	-	Subordinate,Visual	-0.549	0.232	-2.371	0.300

Table A2. continued

Sensory modality × Signaller's sex						
contrast			estimate	SE	z.ratio	*P*
Auditory,F	-	Tactile,F	-0.404	0.146	-2.755	0.065
Auditory,F	-	Visual,F	-0.990	0.150	-6.591	< **0.0001**
Auditory,F	-	Auditory,M	0.077	0.203	0.380	0.999
Tactile,F	-	Visual,F	-0.586	0.111	-5.299	< **0.0001**
Tactile,F	-	Tactile,M	-0.104	0.182	-0.573	0.993
Visual,F	-	Visual,M	0.361	0.180	2.009	0.337
Auditory,M	-	Tactile,M	-0.585	0.176	-3.322	**0.012**
Auditory,M	-	Visual,M	-0.705	0.177	-3.978	**0.001**
Tactile,M	-	Visual,M	-0.120	0.140	-0.858	0.956
Signaller's age class × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
Eld.,Auditory	-	Ado.,Auditory	-1.356	0.342	-3.970	**0.006**
Eld.,Auditory	-	Imm.,Auditory	-0.396	0.384	-1.031	1.000
Eld.,Auditory	-	M.adu.,Auditory	-1.500	0.389	-3.852	**0.010**
Eld.,Auditory	-	Y.adu.,Auditory	-1.141	0.385	-2.962	0.169
Eld.,Auditory	-	Eld.,Tactile	-0.054	0.241	-0.225	1.000
Eld.,Auditory	-	Eld.,Visual	-1.022	0.269	-3.803	**0.012**
Ado.,Auditory	-	Imm.,Auditory	0.960	0.358	2.679	0.318
Ado.,Auditory	-	M.adu.,Auditory	-0.143	0.315	-0.455	1.000
Ado.,Auditory	-	Y.adu.,Auditory	0.215	0.276	0.778	1.000
Ado.,Auditory	-	Ado.,Tactile	-0.262	0.193	-1.357	0.991
Ado.,Auditory	-	Ado.,Visual	-0.342	0.208	-1.648	0.948
Imm.,Auditory	-	M.adu.,Auditory	-1.104	0.422	-2.614	0.360
Imm.,Auditory	-	Y.adu.,Auditory	-0.745	0.393	-1.895	0.856
Imm.,Auditory	-	Imm.,Tactile	-0.502	0.207	-2.417	0.502
Imm.,Auditory	-	Imm.,Visual	-1.071	0.220	-4.857	**0.0001**
M.adu.,Auditory	-	Y.adu.,Auditory	0.358	0.338	1.061	0.999
M.adu.,Auditory	-	M.adu.,Tactile	-0.895	0.253	-3.539	**0.031**
M.adu.,Auditory	-	M.adu.,Visual	-0.878	0.276	-3.176	0.096
Y.adu.,Auditory	-	Y.adu.,Tactile	-0.758	0.210	-3.602	**0.025**
Y.adu.,Auditory	-	Y.adu.,Visual	-0.925	0.230	-4.016	**0.005**
Eld.,Tactile	-	Ado.,Tactile	-1.564	0.297	-5.263	< **0.0001**
Eld.,Tactile	-	Imm.,Tactile	-0.843	0.306	-2.759	0.270
Eld.,Tactile	-	M.adu.,Tactile	-2.340	0.333	-7.023	< **0.0001**
Eld.,Tactile	-	Y.adu.,Tactile	-1.845	0.329	-5.604	< **0.0001**
Eld.,Tactile	-	Eld.,Visual	-0.968	0.216	-4.484	**0.001**
Ado.,Tactile	-	Imm.,Tactile	0.720	0.293	2.458	0.471
Ado.,Tactile	-	M.adu.,Tactile	-0.777	0.269	-2.890	0.201
Ado.,Tactile	-	Y.adu.,Tactile	-0.282	0.236	-1.195	0.997
Ado.,Tactile	-	Ado.,Visual	-0.080	0.158	-0.507	1.000
Imm.,Tactile	-	M.adu.,Tactile	-1.497	0.344	-4.356	**0.001**
Imm.,Tactile	-	Y.adu.,Tactile	-1.002	0.319	-3.140	0.106
Imm.,Tactile	-	Imm.,Visual	-0.569	0.167	-3.406	**0.048**
M.adu.,Tactile	-	Y.adu.,Tactile	0.495	0.279	1.778	0.907
M.adu.,Tactile	-	M.adu.,Visual	0.017	0.210	0.083	1.000
Y.adu.,Tactile	-	Y.adu.,Visual	-0.167	0.166	-1.007	1.000
Eld.,Visual	-	Ado.,Visual	-0.676	0.286	-2.366	0.541
Eld.,Visual	-	Imm.,Visual	-0.445	0.303	-1.468	0.981
Eld.,Visual	-	M.adu.,Visual	-1.355	0.314	-4.318	**0.002**
Eld.,Visual	-	Y.adu.,Visual	-1.044	0.318	-3.279	0.071
Ado.,Visual	-	Imm.,Visual	0.231	0.289	0.799	1.000
Ado.,Visual	-	M.adu.,Visual	-0.679	0.265	-2.565	0.394
Ado.,Visual	-	Y.adu.,Visual	-0.368	0.236	-1.558	0.967
Imm.,Visual	-	M.adu.,Visual	-0.911	0.330	-2.759	0.269
Imm.,Visual	-	Y.adu.,Visual	-0.599	0.319	-1.876	0.865
M.adu.,Visual	-	Y.adu.,Visual	0.311	0.276	1.130	0.999

Table A2. continued

SVF × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
R,Auditory	-	L,Auditory	-0.679	0.127	-5.364	< **0.0001**
R,Auditory	-	R,Tactile	-1.880	0.155	-12.158	< **0.0001**
R,Auditory	-	R,Visual	-2.131	0.171	-12.433	< **0.0001**
L,Auditory	-	L,Tactile	0.891	0.147	6.060	< **0.0001**
L,Auditory	-	L,Visual	0.436	0.156	2.791	0.059
R,Tactile	-	L,Tactile	2.092	0.086	24.446	< **0.0001**
R,Tactile	-	R,Visual	-0.251	0.129	-1.950	0.372
L,Tactile	-	L,Visual	-0.455	0.114	-4.005	**0.001**
R,Visual	-	L,Visual	1.888	0.074	25.660	< **0.0001**
RVF × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
R,Auditory	-	L,Auditory	-0.725	0.133	-5.444	< **0.0001**
R,Auditory	-	R,Tactile	-0.396	0.150	-2.643	0.087
R,Auditory	-	R,Visual	-1.266	0.164	-7.730	< **0.0001**
L,Auditory	-	L,Tactile	-0.593	0.152	-3.914	**0.001**
L,Auditory	-	L,Visual	-0.429	0.162	-2.644	0.087
R,Tactile	-	L,Tactile	-0.922	0.092	-10.061	< **0.0001**
R,Tactile	-	R,Visual	-0.871	0.121	-7.192	< **0.0001**
L,Tactile	-	L,Visual	0.164	0.120	1.363	0.749
R,Visual	-	L,Visual	0.112	0.082	1.377	0.741
Emotion × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
N,Auditory	-	P,Auditory	0.103	0.244	0.422	0.998
N,Auditory	-	N,Tactile	-0.711	0.181	-3.920	**0.001**
N,Auditory	-	N,Visual	-0.938	0.193	-4.857	< **0.0001**
P,Auditory	-	P,Tactile	-0.278	0.141	-1.969	0.360
P,Auditory	-	P,Visual	-0.757	0.152	-4.977	< **0.0001**
N,Tactile	-	P,Tactile	0.536	0.233	2.303	0.193
N,Tactile	-	N,Visual	-0.227	0.164	-1.383	0.737
P,Tactile	-	P,Visual	-0.479	0.094	-5.101	< **0.0001**
N,Visual	-	P,Visual	0.284	0.212	1.343	0.761
Sensory modality × Recipient's hierarchical rank						
contrast			estimate	SE	z.ratio	*P*
Auditory,Dominant	-	Tactile,Dominant	-0.547	0.150	-3.649	**0.008**
Auditory,Dominant	-	Visual,Dominant	-1.009	0.158	-6.396	< **0.0001**
Auditory,Dominant	-	Auditory,Intermediate	-0.152	0.111	-1.371	0.909
Auditory,Dominant	-	Auditory,Subordinate	0.054	0.117	0.461	1.000
Tactile,Dominant	-	Visual,Dominant	-0.462	0.118	-3.932	**0.003**
Tactile,Dominant	-	Tactile,Intermediate	0.014	0.092	0.151	1.000
Tactile,Dominant	-	Tactile,Subordinate	0.047	0.097	0.482	1.000
Visual,Dominant	-	Visual,Intermediate	0.228	0.087	2.618	0.179
Visual,Dominant	-	Visual,Subordinate	0.160	0.100	1.603	0.804
Auditory,Intermediate	-	Tactile,Intermediate	-0.382	0.160	-2.385	0.292
Auditory,Intermediate	-	Visual,Intermediate	-0.630	0.167	-3.777	**0.005**
Auditory,Intermediate	-	Auditory,Subordinate	0.206	0.108	1.903	0.612
Tactile,Intermediate	-	Visual,Intermediate	-0.249	0.124	-2.008	0.538
Tactile,Intermediate	-	Tactile,Subordinate	0.033	0.089	0.372	1.000
Visual,Intermediate	-	Visual,Subordinate	-0.068	0.083	-0.815	0.997
Auditory,Subordinate	-	Tactile,Subordinate	-0.554	0.151	-3.669	**0.008**
Auditory,Subordinate	-	Visual,Subordinate	-0.903	0.160	-5.655	< **0.0001**
Tactile,Subordinate	-	Visual,Subordinate	-0.349	0.115	-3.036	0.061

Table A2. continued

Zoo × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
Leipzig,Auditory	-	Beauval,Auditory	-0.703	0.202	-3.482	**0.015**
Leipzig,Auditory	-	Palmyre,Auditory	-0.410	0.193	-2.121	0.459
Leipzig,Auditory	-	Leipzig,Tactile	-0.928	0.134	-6.919	< **0.0001**
Leipzig,Auditory	-	Leipzig,Visual	-1.450	0.146	-9.959	< **0.0001**
Beauval,Auditory	-	Palmyre,Auditory	0.293	0.218	1.345	0.918
Beauval,Auditory	-	Beauval,Tactile	-0.401	0.168	-2.384	0.293
Beauval,Auditory	-	Beauval,Visual	-0.577	0.170	-3.392	**0.020**
Palmyre,Auditory	-	Palmyre,Tactile	-0.154	0.180	-0.855	0.995
Palmyre,Auditory	-	Palmyre,Visual	-0.516	0.186	-2.769	0.125
Leipzig,Tactile	-	Beauval,Tactile	-0.175	0.173	-1.013	0.985
Leipzig,Tactile	-	Palmyre,Tactile	0.364	0.167	2.183	0.417
Leipzig,Tactile	-	Leipzig,Visual	-0.521	0.107	-4.873	< **0.0001**
Beauval,Tactile	-	Palmyre,Tactile	0.540	0.190	2.842	0.104
Beauval,Tactile	-	Beauval,Visual	-0.176	0.133	-1.329	0.923
Palmyre,Tactile	-	Palmyre,Visual	-0.363	0.135	-2.680	0.155
Leipzig,Visual	-	Beauval,Visual	0.170	0.177	0.957	0.990
Leipzig,Visual	-	Palmyre,Visual	0.523	0.170	3.079	0.054
Beauval,Visual	-	Palmyre,Visual	0.353	0.191	1.853	0.646
Signaller's sex × Duration						
contrast			estimate	SE	z.ratio	*P*
F,Long	-	M,Long	0.282	0.180	1.570	0.396
F,Long	-	F,Short	0.442	0.215	2.060	0.166
M,Long	-	M,Short	0.100	0.201	0.500	0.959
F,Short	-	M,Short	-0.060	0.167	-0.357	0.985
SVF × Duration						
contrast			estimate	SE	z.ratio	*P*
R,Long	-	L,Long	1.287	0.099	13.054	< **0.0001**
R,Long	-	R,Short	0.458	0.209	2.194	0.125
L,Long	-	L,Short	0.085	0.209	0.408	0.977
R,Short	-	L,Short	0.914	0.059	15.455	< **0.0001**
RVF × Duration						
contrast			estimate	SE	z.ratio	*P*
R,Long	-	L,Long	-0.804	0.104	-7.709	< **0.0001**
R,Long	-	R,Short	-0.021	0.207	-0.103	1.000
L,Long	-	L,Short	0.564	0.210	2.684	**0.037**
R,Short	-	L,Short	-0.219	0.073	-2.991	**0.015**
Emotion × Duration						
contrast			estimate	SE	z.ratio	*P*
N,Long	-	P,Long	0.777	0.386	2.016	0.182
N,Long	-	N,Short	0.741	0.396	1.868	0.242
P,Long	-	P,Short	-0.198	0.062	-3.180	**0.008**
N,Short	-	P,Short	-0.162	0.127	-1.267	0.584

Table A2. continued

Signaller's age class × Use of communication tool						
contrast			estimate	SE	z.ratio	*P*
Eld.,No	-	Ado.,No	-0.595	0.279	-2.129	0.507
Eld.,No	-	Imm.,No	-0.045	0.290	-0.155	1.000
Eld.,No	-	M.adu.,No	-1.105	0.304	-3.636	**0.010**
Eld.,No	-	Y.adu.,No	-0.638	0.311	-2.051	0.563
Eld.,No	-	Eld.,Yes	1.586	0.211	7.523	< **0.0001**
Ado.,No	-	Imm.,No	0.550	0.279	1.974	0.618
Ado.,No	-	M.adu.,No	-0.510	0.245	-2.077	0.544
Ado.,No	-	Y.adu.,No	-0.043	0.227	-0.191	1.000
Ado.,No	-	Ado.,Yes	0.379	0.115	3.289	**0.034**
Imm.,No	-	M.adu.,No	-1.060	0.314	-3.380	**0.025**
Imm.,No	-	Y.adu.,No	-0.593	0.305	-1.945	0.638
Imm.,No	-	Imm.,Yes	0.554	0.125	4.436	**0.0004**
M.adu.,No	-	Y.adu.,No	0.467	0.255	1.833	0.714
M.adu.,No	-	M.adu.,Yes	0.332	0.203	1.635	0.831
Y.adu.,No	-	Y.adu.,Yes	0.176	0.169	1.043	0.990
Eld.,Yes	-	Ado.,Yes	-1.802	0.316	-5.711	< **0.0001**
Eld.,Yes	-	Imm.,Yes	-1.077	0.330	-3.268	**0.036**
Eld.,Yes	-	M.adu.,Yes	-2.359	0.365	-6.466	< **0.0001**
Eld.,Yes	-	Y.adu.,Yes	-2.049	0.354	-5.795	< **0.0001**
Ado.,Yes	-	Imm.,Yes	0.725	0.289	2.508	0.264
Ado.,Yes	-	M.adu.,Yes	-0.557	0.292	-1.903	0.667
Ado.,Yes	-	Y.adu.,Yes	-0.246	0.255	-0.965	0.994
Imm.,Yes	-	M.adu.,Yes	-1.281	0.352	-3.638	**0.010**
Imm.,Yes	-	Y.adu.,Yes	-0.971	0.330	-2.942	0.095
M.adu.,Yes	-	Y.adu.,Yes	0.310	0.314	0.987	0.993
SVF × Use of communication tool						
contrast			estimate	SE	z.ratio	*P*
R,No	-	L,No	2.402	0.056	42.888	< **0.0001**
R,No	-	R,Yes	1.907	0.116	16.425	< **0.0001**
L,No	-	L,Yes	-0.696	0.096	-7.266	< **0.0001**
R,Yes	-	L,Yes	-0.201	0.114	-1.762	0.292
RVF × Use of communication tool						
contrast			estimate	SE	z.ratio	*P*
R,No	-	L,No	-0.211	0.067	-3.165	**0.009**
R,No	-	R,Yes	0.906	0.106	8.536	< **0.0001**
L,No	-	L,Yes	0.304	0.104	2.918	**0.019**
R,Yes	-	L,Yes	-0.813	0.120	-6.765	< **0.0001**
Emotion × Use of communication tool						
contrast			estimate	SE	z.ratio	*P*
N,No	-	P,No	0.465	0.213	2.181	0.129
N,No	-	N,Yes	0.763	0.133	5.716	< **0.0001**
P,No	-	P,Yes	0.448	0.097	4.600	< **0.0001**
N,Yes	-	P,Yes	0.150	0.230	0.654	0.914
RVF × Signaller's hierarchical rank						
contrast			estimate	SE	z.ratio	*P*
R,Dominant	-	L,Dominant	-0.612	0.089	-6.849	< **0.0001**
R,Dominant	-	R,Intermediate	-0.200	0.212	-0.944	0.935
R,Dominant	-	R,Subordinate	-0.716	0.273	-2.626	0.091
L,Dominant	-	L,Intermediate	0.057	0.214	0.268	1.000
L,Dominant	-	L,Subordinate	-0.671	0.278	-2.413	0.152
R,Intermediate	-	L,Intermediate	-0.355	0.115	-3.090	**0.025**
R,Intermediate	-	R,Subordinate	-0.516	0.231	-2.236	0.221
L,Intermediate	-	L,Subordinate	-0.728	0.237	-3.079	**0.025**
R,Subordinate	-	L,Subordinate	-0.567	0.123	-4.595	**0.0001**

Table A2. continued

RVF × Signaller's age class						
contrast			estimate	SE	z.ratio	*P*
R,Eld.	-	L,Eld.	-0.265	0.146	-1.812	0.728
R,Eld.	-	R,Ado.	-0.913	0.283	-3.222	**0.042**
R,Eld.	-	R,Imm.	-0.481	0.294	-1.635	0.831
R,Eld.	-	R,M.adu.	-1.744	0.315	-5.541	< **0.0001**
R,Eld.	-	R,Y.adu.	-1.079	0.318	-3.398	0.024
L,Eld.	-	L,Ado.	-1.484	0.288	-5.153	< **0.0001**
L,Eld.	-	L,Imm.	-0.641	0.300	-2.136	0.502
L,Eld.	-	L,M.adu.	-1.719	0.318	-5.405	< **0.0001**
L,Eld.	-	L,Y.adu.	-1.608	0.322	-4.992	< **0.0001**
R,Ado.	-	L,Ado.	-0.836	0.113	-7.418	< **0.0001**
R,Ado.	-	R,Imm.	0.432	0.283	1.527	0.882
R,Ado.	-	R,M.adu.	-0.831	0.255	-3.258	**0.037**
R,Ado.	-	R,Y.adu.	-0.166	0.228	-0.727	0.999
L,Ado.	-	L,Imm.	0.843	0.289	2.921	0.100
L,Ado.	-	L,M.adu.	-0.235	0.258	-0.911	0.996
L,Ado.	-	L,Y.adu.	-0.124	0.231	-0.536	1.000
R,Imm.	-	L,Imm.	-0.424	0.108	-3.931	**0.003**
R,Imm.	-	R,M.adu.	-1.263	0.322	-3.919	**0.004**
R,Imm.	-	R,Y.adu.	-0.598	0.312	-1.917	0.657
L,Imm.	-	L,M.adu.	-1.078	0.328	-3.284	**0.035**
L,Imm.	-	L,Y.adu.	-0.967	0.318	-3.043	0.071
R,M.adu.	-	L,M.adu.	-0.240	0.141	-1.704	0.794
R,M.adu.	-	R,Y.adu.	0.665	0.267	2.490	0.274
L,M.adu.	-	L,Y.adu.	0.111	0.271	0.412	1.000
R,Y.adu.	-	L,Y.adu.	-0.794	0.132	-6.014	< **0.0001**
RVF × Zoo						
contrast			estimate	SE	z.ratio	*P*
R,Leipzig	-	L,Leipzig	-0.367	0.081	-4.548	**0.0001**
R,Leipzig	-	R,Beauval	-0.081	0.174	-0.467	0.997
R,Leipzig	-	R,Palmyre	0.222	0.166	1.337	0.764
L,Leipzig	-	L,Beauval	-0.391	0.176	-2.227	0.225
L,Leipzig	-	L,Palmyre	0.096	0.166	0.579	0.992
R,Beauval	-	L,Beauval	-0.676	0.099	-6.848	< **0.0001**
R,Beauval	-	R,Palmyre	0.303	0.188	1.617	0.587
L,Beauval	-	L,Palmyre	0.488	0.189	2.575	0.104
R,Palmyre	-	L,Palmyre	-0.492	0.098	-5.038	< **0.0001**
SVF × Signaller's hierarchical rank						
contrast			estimate	SE	z.ratio	*P*
R,Dominant	-	L,Dominant	0.853	0.077	11.112	< **0.0001**
R,Dominant	-	R,Intermediate	-0.301	0.213	-1.417	0.717
R,Dominant	-	R,Subordinate	-0.834	0.268	-3.111	**0.023**
L,Dominant	-	L,Intermediate	0.159	0.210	0.757	0.975
L,Dominant	-	L,Subordinate	-0.553	0.268	-2.065	0.306
R,Intermediate	-	L,Intermediate	1.314	0.108	12.143	< **0.0001**
R,Intermediate	-	R,Subordinate	-0.532	0.229	-2.324	0.185
L,Intermediate	-	L,Subordinate	-0.712	0.226	-3.155	**0.020**
R,Subordinate	-	L,Subordinate	1.134	0.063	18.065	< **0.0001**

Table A2. continued

SVF × Zoo						
contrast			estimate	SE	z.ratio	*P*
R,Leipzig	-	L,Leipzig	0.813	0.071	11.395	< **0.0001**
R,Leipzig	-	R,Beauval	-0.436	0.177	-2.467	0.134
R,Leipzig	-	R,Palmyre	-0.072	0.168	-0.429	0.998
L,Leipzig	-	L,Beauval	-0.037	0.173	-0.213	1.000
L,Leipzig	-	L,Palmyre	0.390	0.165	2.361	0.170
R,Beauval	-	L,Beauval	1.212	0.093	13.099	< **0.0001**
R,Beauval	-	R,Palmyre	0.364	0.189	1.921	0.389
L,Beauval	-	L,Palmyre	0.427	0.186	2.294	0.196
R,Palmyre	-	L,Palmyre	1.276	0.085	15.097	< **0.0001**
Affiliation × Signaller's age class						
contrast			estimate	SE	z.ratio	*P*
Strong,Eld.	-	Low,Eld.	-0.511	0.264	-1.932	0.837
Strong,Eld.	-	Medium,Eld.	-0.089	0.290	-0.306	1.000
Strong,Eld.	-	Strong,Ado.	-1.254	0.357	-3.511	**0.034**
Strong,Eld.	-	Strong,Imm.	-0.895	0.336	-2.664	0.327
Strong,Eld.	-	Strong,M.adu.	-1.797	0.412	-4.360	**0.001**
Strong,Eld.	-	Strong,Y.adu.	-1.295	0.410	-3.156	0.101
Low,Eld.	-	Medium,Eld.	0.422	0.205	2.061	0.761
Low,Eld.	-	Low,Ado.	-0.755	0.272	-2.770	0.264
Low,Eld.	-	Low,Imm.	-0.255	0.293	-0.870	1.000
Low,Eld.	-	Low,M.adu.	-1.351	0.291	-4.638	**0.0004**
Low,Eld.	-	Low,Y.adu.	-1.208	0.298	-4.054	**0.005**
Medium,Eld.	-	Medium,Ado.	-1.587	0.335	-4.738	**0.0002**
Medium,Eld.	-	Medium,Imm.	-0.534	0.333	-1.606	0.958
Medium,Eld.	-	Medium,M.adu.	-2.047	0.367	-5.582	< **0.0001**
Medium,Eld.	-	Medium,Y.adu.	-1.527	0.361	-4.231	**0.002**
Strong,Ado.	-	Low,Ado.	-0.011	0.151	-0.076	1.000
Strong,Ado.	-	Medium,Ado.	-0.422	0.178	-2.370	0.537
Strong,Ado.	-	Strong,Imm.	0.359	0.307	1.169	0.998
Strong,Ado.	-	Strong,M.adu.	-0.543	0.315	-1.725	0.926
Strong,Ado.	-	Strong,Y.adu.	-0.041	0.281	-0.147	1.000
Low,Ado.	-	Medium,Ado.	-0.411	0.152	-2.704	0.303
Low,Ado.	-	Low,Imm.	0.500	0.284	1.759	0.914
Low,Ado.	-	Low,M.adu.	-0.596	0.241	-2.470	0.462
Low,Ado.	-	Low,Y.adu.	-0.454	0.223	-2.040	0.775
Medium,Ado.	-	Medium,Imm.	1.053	0.334	3.157	0.101
Medium,Ado.	-	Medium,M.adu.	-0.460	0.275	-1.671	0.942
Medium,Ado.	-	Medium,Y.adu.	0.061	0.241	0.251	1.000
Strong,Imm.	-	Low,Imm.	0.129	0.140	0.918	1.000
Strong,Imm.	-	Medium,Imm.	0.272	0.181	1.498	0.977
Strong,Imm.	-	Strong,M.adu.	-0.903	0.380	-2.377	0.532
Strong,Imm.	-	Strong,Y.adu.	-0.400	0.369	-1.085	0.999
Low,Imm.	-	Medium,Imm.	0.143	0.163	0.876	1.000
Low,Imm.	-	Low,M.adu.	-1.096	0.308	-3.557	**0.029**
Low,Imm.	-	Low,Y.adu.	-0.953	0.303	-3.148	0.104
Medium,Imm.	-	Medium,M.adu.	-1.513	0.369	-4.097	**0.004**
Medium,Imm.	-	Medium,Y.adu.	-0.993	0.351	-2.831	0.230
Strong,M.adu.	-	Low,M.adu.	-0.064	0.212	-0.303	1.000
Strong,M.adu.	-	Medium,M.adu.	-0.339	0.248	-1.365	0.990
Strong,M.adu.	-	Strong,Y.adu.	0.502	0.344	1.462	0.981
Low,M.adu.	-	Medium,M.adu.	-0.275	0.187	-1.466	0.981
Low,M.adu.	-	Low,Y.adu.	0.142	0.248	0.573	1.000
Medium,M.adu.	-	Medium,Y.adu.	0.521	0.289	1.799	0.899
Strong,Y.adu.	-	Low,Y.adu.	-0.424	0.205	-2.067	0.757
Strong,Y.adu.	-	Medium,Y.adu.	-0.320	0.231	-1.385	0.989
Low,Y.adu.	-	Medium,Y.adu.	0.104	0.159	0.653	1.000

Table A2. continued

Signaller's hierarchical rank × Affiliation						
contrast			estimate	SE	z.ratio	*P*
Dominant,Strong	-	Intermediate,Strong	0.030	0.270	0.111	1.000
Dominant,Strong	-	Subordinate,Strong	-0.281	0.303	-0.928	0.991
Dominant,Strong	-	Dominant,Low	-0.042	0.144	-0.290	1.000
Dominant,Strong	-	Dominant,Medium	0.199	0.166	1.204	0.956
Intermediate,Strong	-	Subordinate,Strong	-0.311	0.272	-1.145	0.967
Intermediate,Strong	-	Intermediate,Low	-0.077	0.178	-0.434	1.000
Intermediate,Strong	-	Intermediate,Medium	-0.069	0.202	-0.341	1.000
Subordinate,Strong	-	Subordinate,Low	-0.410	0.148	-2.770	0.124
Subordinate,Strong	-	Subordinate,Medium	-0.670	0.196	-3.422	**0.018**
Dominant,Low	-	Intermediate,Low	-0.005	0.206	-0.027	1.000
Dominant,Low	-	Subordinate,Low	-0.649	0.271	-2.393	0.288
Dominant,Low	-	Dominant,Medium	0.241	0.128	1.876	0.631
Intermediate,Low	-	Subordinate,Low	-0.644	0.224	-2.874	0.095
Intermediate,Low	-	Intermediate,Medium	0.008	0.147	0.057	1.000
Subordinate,Low	-	Subordinate,Medium	-0.260	0.181	-1.434	0.885
Dominant,Medium	-	Intermediate,Medium	-0.238	0.228	-1.044	0.982
Dominant,Medium	-	Subordinate,Medium	-1.150	0.322	-3.568	**0.011**
Intermediate,Medium	-	Subordinate,Medium	-0.912	0.275	-3.317	**0.026**

Figure captions

Figure 1: Positions of recipient in relation to signaller during an interaction. Heads of subjects represented by arrows (oriented ahead of subjects). Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field. Recipient's Visual Fields: signaller in recipient's left (RVF_L) or right (RVF_R) visual field. Dotted lines: recipient, unbroken lines: signaller, bold lines: left hemiface, thin lines: right hemiface. The different possible positions are ordered in increasing frequency of occurrence.

Figure 2: Adjusted probability (± SE) of right-hand use for each sensory modality. (a) Interaction with Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field; (b) Interaction with Recipient's Visual Fields: signaller in recipient's left (RVF_L) or right (RVF_R) visual field. Vertically striped bars: tactile gestures. Squared bars: auditory gestures. Diagonally striped bars: visual gestures. Tukey tests: $**P < 0.01$, $***P < 0.001$.

Figure 3: Adjusted probability (± SE) of right-hand use for gestures with and without an **object according to (a) the position of the recipient in the signaller's visual field and (b) conversely.** (a) Interactions with Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field. (b) Interaction with Recipient's Visual Fields: signaller in recipient's left (RVF_L) or right (RVF_R) visual field. Grey bars: Gestures with object. Diagonally striped bars: Gestures without object. Tukey tests: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Figure 4: **Adjusted probability (± S.E.) of right-hand use for each signaller's hierarchical rank.** (a) Interactions with Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field. (b) Interaction with Recipient's Visual Fields: signaller in recipient's left (RVF_L) or right (RVF_R) visual field. Black bars: left visual field. Open bars: right visual field. Tukey tests: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Figure 5: Adjusted probability (± SE) of right-hand use for each sharing degree. Interactions with emotional context: Horizontally striped bars: common gestures. Stippled bars: rare gestures. Tukey test: $*P < 0.05$.

Figure 6: Adjusted probability (± SE) of right-hand use for each signaller's age class. Interactions with Recipient's Visual Fields: signaller in recipient's left (RVF_L) or right (RVF_R) visual field (a) between RVF (b) within RVF. Gradual range of grey bars: age classes from light grey (Immature) to dark grey (Elder). Black bars: left visual field. Open bars: right visual field. Tukey tests: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Figure 7: Adjusted probability (± SE) of right-hand use for each sensory modality. Interactions with (a) signaller's hierarchical rank and (b) recipient's hierarchical rank: Vertically striped bars: tactile gestures. Squared bars: auditory gestures. Diagonally striped bars: visual gestures. Tukey tests: $*P < 0.05$ $**P < 0.01$, $***P < 0.001$.

Figure 1

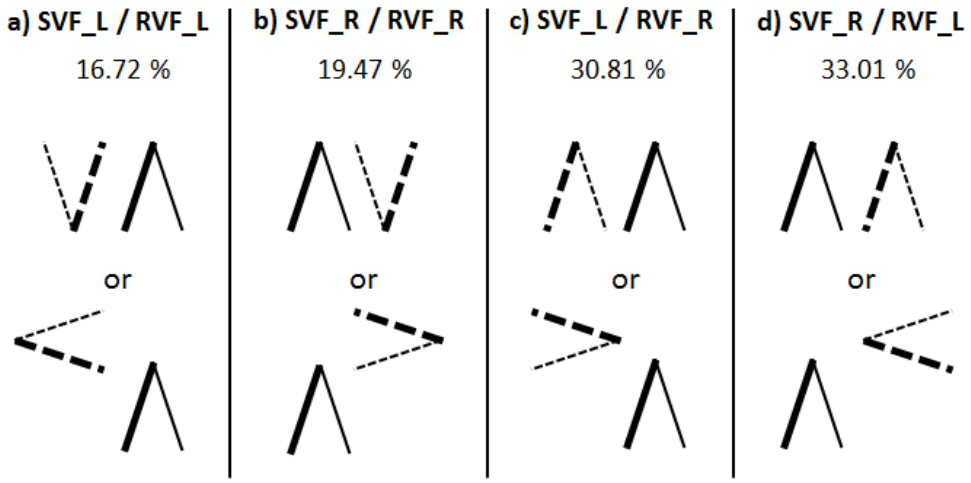


Figure 2

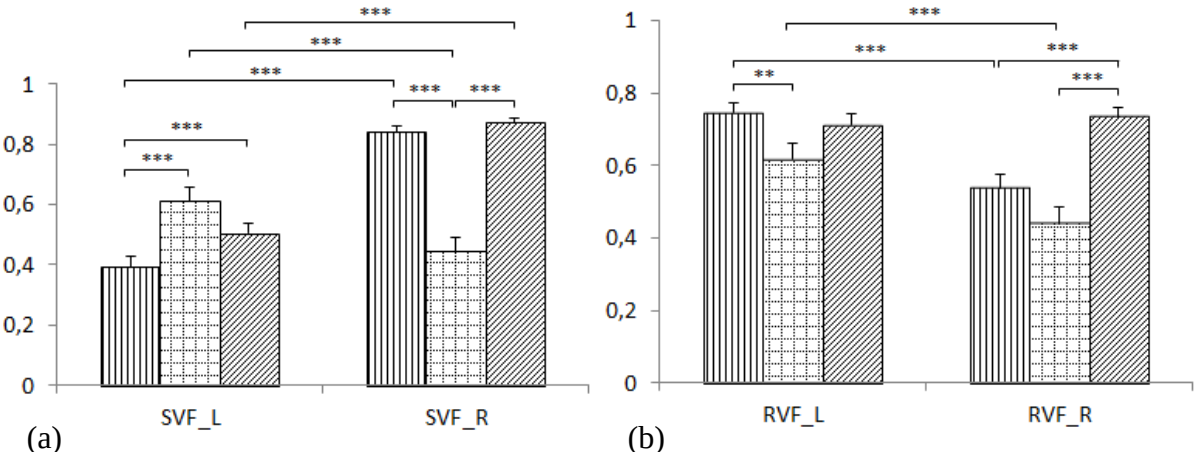


Figure 3

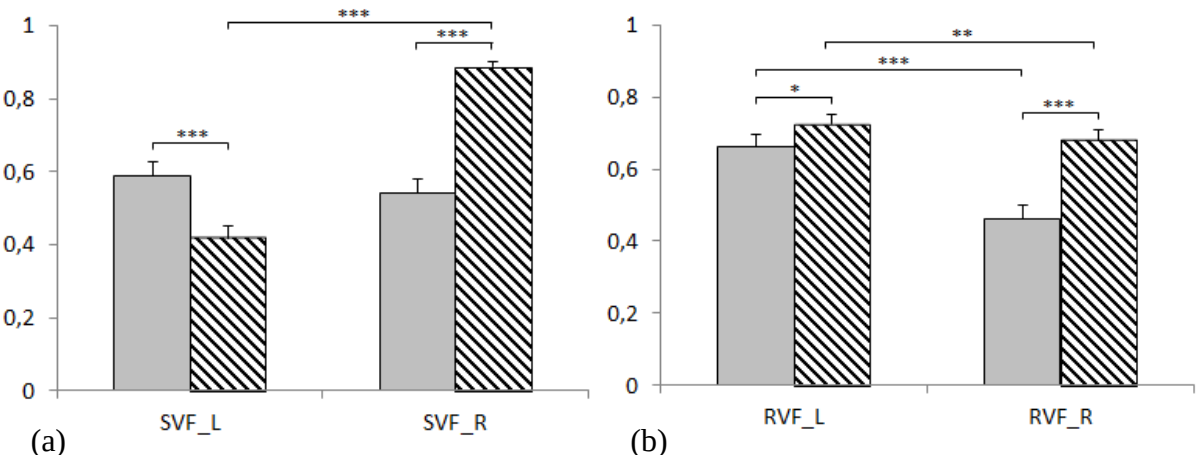


Figure 4

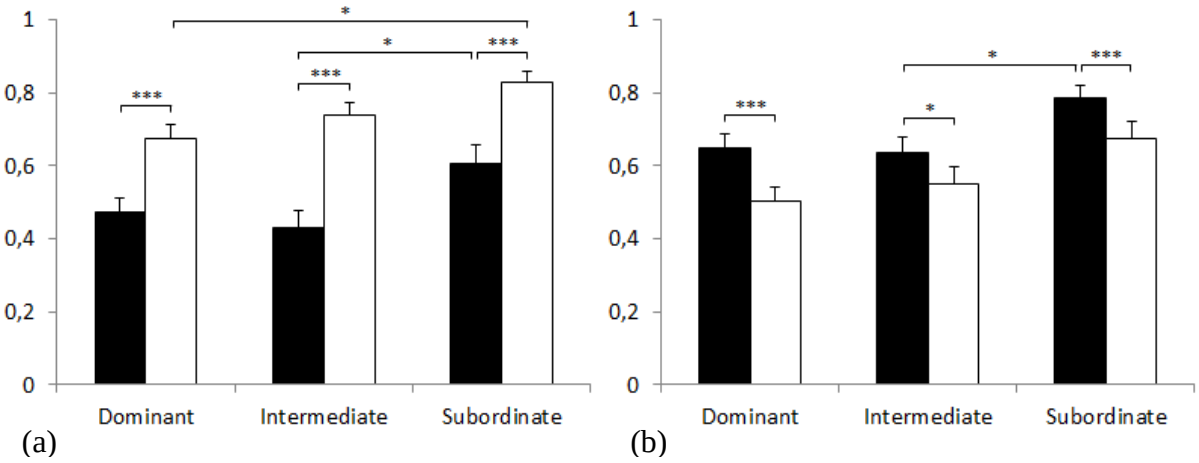


Figure 5

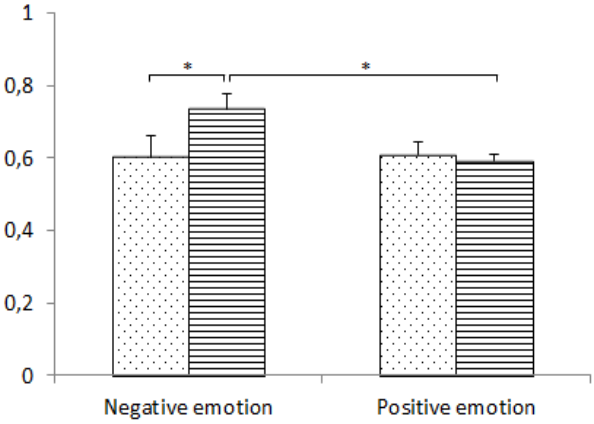


Figure 6

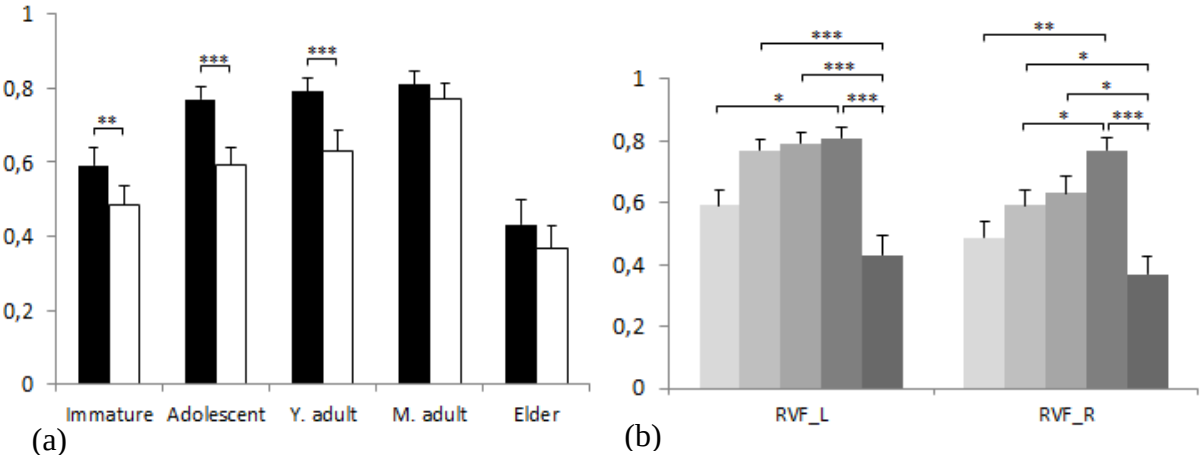
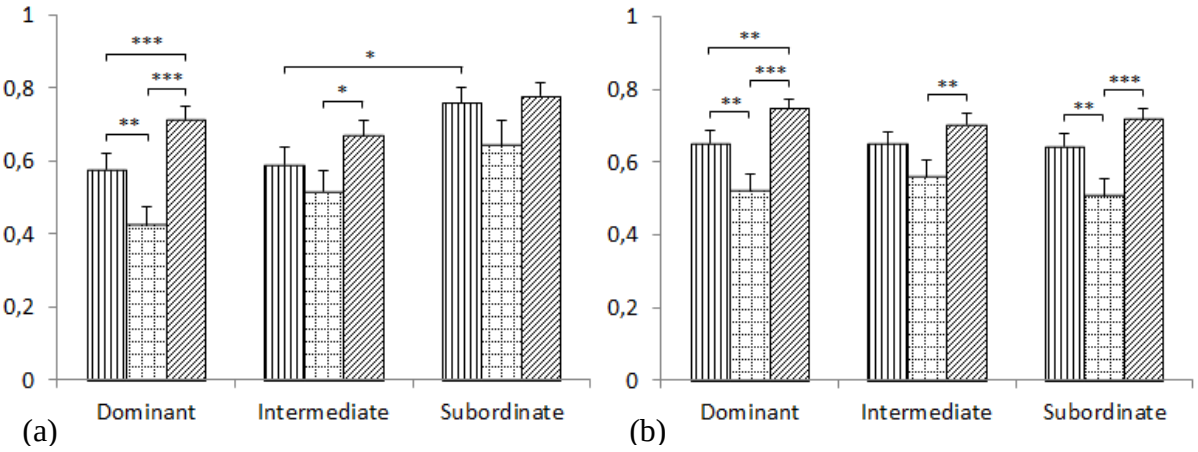


Figure 7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Intermediate
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Dominant
Intermediate
Subordinate
(b)

Article 2

Manuscript to be submitted to American Journal of Physical Anthropology

Captive gorillas' intraspecific gestural laterality: evidence of a population-level right-hand bias and multifactorial investigation

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Summary of Article 2

Questions: An ever-growing body of research focuses on potential continuities and discontinuities between human and non-human primates' gestural laterality. To our knowledge, the present study is the first to investigate gorillas' laterality in purely intraspecific gestural communication. Within a comparative approach, we studied gorillas' intraspecific gestural laterality using a methodological procedure identical to the one implemented for chimpanzees presented in Article 1. Thus, we analysed, first, the most frequent gesture types of gorillas' communication repertoire. Second, we used a multifactorial analysis to assess and to compare the effects of various potential influential factors affecting their gestural laterality. We asked two questions. Is there a gestural laterality bias at the population level? Which factors influence gestural laterality?

Methods: We investigated intraspecific gestural laterality in dyadic interactions in three groups of gorillas (N=35) in real-life social-ecological relevant contexts. First, we analysed each of the 16 gestures separately. Second, we assessed gorillas' gestural laterality taking into account simultaneously potential influential factors: interactional context components (visual field and body side of both signaller and recipient as well as the emotional valence of context), gesture characteristics (sensory modality, use of communication tool, duration, and degree of sharing) and individual sociodemographic characteristics of both signaller and recipient (age, sex, group/zoo, hierarchy, kinship and affiliation).

Results: We found that, at the population level, 9 of the 16 gestures we observed were performed predominantly by the right hand. Our multivariate study showed that gorilla signallers used their hand ipsilateral to the recipient for tactile and visual gestures and whatever the emotional context, gesture duration, recipient's sex or the dyadic kin relationship between signaller and recipient, and whether or not a communication tool was used. Signallers' did not use their contralateral hand predominantly in any situation. Furthermore, signallers' right-hand use was particularly pronounced in negative contexts, for short gestures and by female signallers, and its use increased with age.

Conclusion: As far as we know, this study is the first to evidence a right-hand bias at the population level for a majority of gorillas' frequent purely intraspecific gestures. Our findings support Ghirlanda and colleagues' (2009) model postulating that a population-level bias could be explained by an evolutionary stable strategy based on intraspecific interactions. They also further support the hypothesis that laterality in gestural communication would represent a precursor of the left-hemispheric lateralization of language. Preliminary comparisons between our results for gorillas and for chimpanzees tend to show that social structure and dynamics could explain some differences in gestural laterality between these two species.

Captive gorillas' intraspecific gestural laterality: evidence of a population-level right-hand bias and multifactorial investigation

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Abstract

Multifactorial investigations of intraspecific laterality of primates' gestural communication aim to shed light on factors that underlie the evolutionary origins of human handedness and language. As yet, little is known concerning laterality of gestures in purely intra-specific communication. As far as we know, this study is the first to assess laterality of gorillas' gestural communication using a comprehensive approach taking into consideration the effect of various factors: gestural characteristics (sensory modality, use of a communication tool, sharing degree in the population and duration); interactional context (visual field and body sides of signaller and recipient, and emotional context); and individual socio-demographic characteristics of signaller and recipient (age, sex, group, hierarchy, affiliation and kinship). Two research questions were asked. First, is a gestural laterality bias observed at the population level? Second, which factors influence gestural laterality? To answer them, we studied laterality in dyadic interactions in three groups of gorillas living in captivity (N=35) focusing on their most frequent communication gesture types (N=16). Our study is the first to investigate purely intraspecific gestural communication of gorillas and we revealed a right-hand bias at the population level for a majority of the gestures studied. However, signallers' gestural laterality was influenced by several factors and their mutual intertwinement. They used predominantly their hand ipsilateral to the recipient for tactile and visual gestures, whatever the emotional context, gesture duration, recipient's sex or the kin relationship between the signaller and the recipient, and whether or not a communication tool was used. Signallers' contralateral hand was not preferentially used in any situation. Signallers' right-hand use was more pronounced in negative contexts, in short gestures, when signallers were females and its use increased with age. Our findings support the hypothesis predicting that population-level bias could be explained by an evolutionary stable strategy based on intraspecific interactions. They are also in line with literature evidencing predominant right-hand use in gestural communication by non-human primates and suggesting that gestural laterality would be a prerequisite of the language left-brain specialization.

Keywords: gestural asymmetry, intraspecific interaction, *Gorilla gorilla gorilla*, cerebral lateralization.

Introduction

Functional cerebral assymmetry at the population level is not restricted to humans but widely spread among vertebrates (e.g. reviews; MacNeilage et al. 2009; Ocklenburg & Güntürkün 2012; Rogers & Andrew 2002; Rogers et al. 2013a; Vallortigara & Rogers 2005; Vallortigara et al. 1999, 2011) and invertebrates (e.g. reviews Frasnelli et al. 2013; Frasnelli et al. 2012). The related limb asymmetry has been extensively documented among vertebrates. However, in spite of a growing and substantial set of research, the phylogenetic mechanisms that lead to the overexpression of right-hand use by humans are still difficult to understand. Although humans present a strong preference for right-hand use at the population level (e.g. McManus 2002), non-human limb preference is not obvious and depends on the species. Ströckens and colleagues (2013) showed in their review that among 119 animal species, 61 (51.3%) presented a population-level bias, 20 (16.8%), presented individual-level biases and 38 (31.9%) presented no evidence of laterality. According to the social hypothesis (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005), biases at the individual level would have emerged because they confer cognitive advantages (e.g. Levy 1977; Rogers 2000; Rogers et al. 2004; Tomassi 2009). Thereafter, directional alignment of lateralization at the population level would have been favoured as an Evolutionarily Stable Strategy (ESS) in which individually asymmetrical organisms must coordinate their behaviour with the behaviour of other asymmetrical organisms. This alignment of lateralization at the population level would provide certain disadvantages by making behaviour more predictable for predators and prey (Vallortigara 2006) but also advantages by facilitating intraspecific interactions (Rogers 2000) as for primates (e.g chimpanzees: Prieur et al. submitted, a, b; mangabeys: Baraud et al. 2009). Ghirlanda and colleagues (2009) recently proposed that the pattern of population-level laterality could be explained by an ESS based on a trade-off between competitive and cooperative intraspecific interactions better than by interspecific interactions.

Despite substantial scientific advances concerning the investigation of laterality of limb-use and laterality in social behaviour, further studies are needed for a better understanding of the evolutionary relationship between population level right-handedness and cerebral lateralization of human language. To this end, non-human primates and particularly great apes can provide particularly valuable clues (e.g. Corballis 2002; Mac Neilage 1984; Vauclair 1999; Hopkins 2007; Meguerditchian et al. 2013). Indeed, they are the closest phylogenetic species to humans (e.g. Langergraber et al. 2012; Scally et al. 2012). Moreover,

they present a remarkable resemblance to humans in terms of hand anatomy (e.g. Aiello & Dean 1990; Napier 1962) and manipulation skills (e.g. Byrne et al. 2001; Napier 1960) as well as in terms of neuroanatomical brain asymmetries (e.g. left cerebral hemisphere predominance in the homologs of the human Broca's and Wernicke's areas: Cantalupo & Hopkins 2001; Gannon et al. 1998; Hopkins et al. 2007). Numerous studies have investigated non-human primates hand preference for manipulations and gestural communication (e.g. Cashmore et al. 2008; Fagot & Vauclair 1991; Fagard 2004; Forrester et al. 2013; Hopkins 2006; Hopkins & Cantalupo 2005; Hopkins et al. 2012; Marchant & McGrew 1991; McGrew & Marchant 1997a; Meguerditchian et al. 2011; Meguerditchian et al. 2013; Papademetriou et al. 2005; Prieur et al. submitted, a, b).

In the present study, the term "gesture" is restricted to communication and defined as "movements of the limbs or head and body directed towards a recipient that are goal-directed, mechanically ineffective (that is, they are not designed to act as direct physical agents) and receive a voluntary response" (Pika & Bugnyar 2011; p 4). From the above-mentioned studies, it appears first that little is known about laterality of gestures in purely intra-specific communication (chimpanzees: Fletcher & Weghorst 2005; Meguerditchian et al. 2010; Hobaiter & Byrne 2013; Prieur et al. submitted, a, b; bonobos: Chapelain 2010; olive baboons: Meguerditchian & Vauclair 2006) compared to gestures directed towards humans or towards both conspecifics and humans (pooled data) although such investigation in real-life socially relevant contexts is particularly interesting from an evolutionary prospect because natural selection operated in comparable contexts.

Second, these studies highlight several methodological issues as well as inconsistencies between studies that make comparisons difficult, such as terminology, method of evaluation (i.e. spontaneous actions or experimental tasks, function - for communication or not -, gestures directed towards humans and/or conspecifics), setting (captivity or wild) as well as data recording and analysis procedures (sample size, number of data per subject, independence of data, factors considered and statistical tests). To avoid biases yielding ambiguous results, it appears thus necessary to adopt standardized methods and to consider large sample size and number of data points per subject, independence of data, multiple potentially influential factors considered and powerful statistical analysis allowing assessing the respective influence of these factors and their interactions. Such approach will be used in the present study.

Third, the relevant literature indicates that many factors can modulate direction, strength and/or consistency of manual laterality (both within and across subjects and both

within and across tasks) of non-human primates including New World and Old World monkeys and great apes. Among factors modulating manual laterality of gestures, we can quote the 3 following categories already considered in our previous study of chimpanzees' intraspecific gestural laterality (Prieur et al. submitted, a): first, interactional context including the relative positions of social partners (i.e. signaller and recipient) during an interaction (Hopkins & Wesley 2002; Bourjade et al. 2013) and emotional context (Casperd & Dunbar 1996; Chapelain 2010); second, type of gestures (Hopkins and Leavens 1998; Hopkins & Wesley 2002; Hobaiter & Byrne 2013) including their characteristics (use of a communication tool or not: Hobaiter & Byrne 2013), sensory modality, sharing degree between group members and duration); third, subjects' demographic characteristics (age, sex: e.g. see review by Meguerditchian et al. 2013; group: Hopkins et al. 2004, 2005b; Meguerditchian 2011, 2012; Prieur et al. submitted, b) and social characteristics (kinship: e.g. Hopkins et al. 1999, 2000, 2001; Damerose & Vauclair 2002; hierarchy: Baraud et al. 2009; Prieur et al. submitted, b; affiliation). As for humans (e.g. Healey et al. 1986; Steenhuis & Bryden 1989), non-human primates' handedness (e.g. Wesley et al. 2002; Prieur et al. submitted, a) appears to be multidimensional. To investigate the origin and functions of human handedness in depth as many potential influential factors as possible must be taken into account using a comprehensive analysis assessing rigorously the distinct influence of each factor on gestural laterality and their interactions. To our knowledge, except our previous investigations on chimpanzees' intraspecific gestural laterality (Prieur et al. submitted, a), no study has assessed laterality by considering simultaneously the effects of the above mentioned influential factors and their interactions as well as taking into account the sociodemographic characteristics of both signaller and recipient, and several narrow categories of age (i.e. infant, juvenile, adolescent, young and mature adult) and rank (i.e. dominant, intermediate and subordinate).

In order to contribute to the understanding of the evolutionary relationship between direction of handedness and left-cerebral lateralization of language, we followed Prieur and colleagues' (submitted, a) methodology for chimpanzees to study gorillas' intraspecific gestural laterality, a species phylogenetically more distant from humans than chimpanzees. As far as we know, only Shafer (1987) investigated gorillas' purely intraspecific gestural communication. However, she considered a category of undistinguished types of hand motions (a category she called "gestures" that did not match our definition of gestures) defined as "any hand motions interpreted as signalling to another gorilla or that were interpreted as solitary gestures" (Shafer 1987, p. 51). She collected 663 data points of

"gestures" but provided no information concerning use of discrete bouts (i.e. sequences of gestures separated by intervals) or frequencies (i.e. every event in a bout) to collect these data (e.g. Marchant & McGrew 1991; Byrne & Byrne 1991). The majority of her subjects who performed "gestures" at least six times (i.e. 18 of 47 gorillas from 5 zoos) were non-lateralized but her results revealed that "gestures" presented a statistical trend towards the right. The present study aimed to explore in depth laterality of gorillas' intraspecific gestural communication by studying their most frequent communication gestures (e.g. Pika et al. 2003, Genty et al. 2009). We wanted to answer the two following questions. First, is there a gestural laterality bias at the population level? Therefore, we analyzed separately each of the 16 gestures considered. As for chimpanzees (Prieur et al. submitted, a), we predicted that a majority of these frequently expressed gestures would be right-lateralized at the population level. Second, which factors influence gestural laterality? To investigate this question, we applied a multifactorial approach considering simultaneously three categories of factors: interactional context components (i.e. visual field and body side of both signaller and recipient and emotional valence of context), gesture characteristics (i.e. sensory modality, use of a communication tool, degree of sharing, and duration), and sociodemographic characteristics of both signaller and recipient (i.e. age, sex, group/zoo, kinship, affiliation, and hierarchy). In agreement with previous studies of other primates, we predicted that gorilla signallers' gestural laterality would be particularly modulated by interactional context, gesture characteristics and social characteristics.

Methods

To comply with the above-mentioned requirement for identical methodologies for all species, the observational procedure and comprehensive statistical analysis used in Prieur et al. (submitted, a, b) for chimpanzees is applied here.

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). Age categories of subjects were based mainly on Breuer and colleagues' (2009) categories for infants (0-3 years), juveniles (4–6 years) and

adolescents (7-11 years) and on Stoinski and colleagues' (2013) categories for young adults (12-20 years) and mature adults (>20 years) (Table 1).

Observation procedures

Observation data were collected at La Vallée des Singes between the18th of May and the 25th of July 2012, at Apenheul Zoo between the 14th of August and the 27th of October 2012 and at Burgers' Zoo between the 29th of April and the 29th of June 2013, respectively during 196.5 h, 214.5 h and 240 h (651 h of observations in all).

Data were collected during four 1.5h sessions per day (two in the morning and two in the afternoon) using "sampling all occurrences of some behaviours" (Altmann 1974). Observation data were collected in real time by using a stopwatch, binoculars, and were recorded on a paper sheet.

Coding procedure

Only intraspecific dyadic interactions were considered. For each of them, we recorded (1) the type of gesture and the hand (left or right) used by the signaller to communicate (based on Pika and colleagues' repertoire 2003), (2) the interactional context of gestural production recording the relative positions of the two subjects before and during an interaction (both visual field and body side) as well as the emotional context (agonistic or affiliative) associated with the interaction, and (3) the identity and role (signaller or recipient) of both subjects, as detailed below.

Following Pika's definition of gesture (Pika 2008a, 2008b), we considered only intentionally produced gestures that (1) were used to initiate (not continue) a social interaction, (2) were mechanically ineffective (Pollick & de Waal 2007), (3) and included gazing at the recipient, gaze alternation, and/or waiting for a response (e.g. Bruner 1981; Tomasello et al. 1989).

We focused on the hand used by the signaller to perform conspecific-directed gestures. A requirement for all hand records was that both the signaller's hands were free and positioned symmetrically with respect to his/her body midline before the interaction, without any environmental factors that could potentially influence the use of one hand (e.g. close to a wall/bush/tree).

Gestures were expressed either singly or in bouts (e.g. Marchant & McGrew 1991; Byrne & Byrne 1991). When expressed in bouts, only the first gesture of the sequence was

recorded. Criteria employed to determine the termination of a gesture or a bout of gestures are the following: the signaller's hand (a) returned to its initial position (Meguerditchian et al. 2010), (b) switched to another non-communication activity (e.g. forage), or (c) the movement was influenced by an outside incident (e.g. stumble) (Hopkins & de Waal 1995; Hopkins et al. 2001a; McGrew & Marchant 2001; Harisson & Nystrom 2010). To ensure statistical independence of data, the required time interval before recording another gesture was set at 3 seconds (Morris et al. 1993; Hopkins & de Waal 1995).

Gesture characteristics

Our gesture classification was based on previous repertoires (when necessary anatomical elements or precisions were added) (Tables 2 and 3). In all, 16 specific gestures were considered and were categorized following Pika and colleagues' (2003, 2005a) descriptions as auditory gestures that generate sound while being performed (n = 4), visual gestures that generate a mainly visual component with no physical contact (n = 6) or tactile gestures that include a physical contact with the recipient (n = 6). These gestures were performed either with (n=4) or without (n=12) an object used as a communication tool. Gesture duration was defined as the delay between the moment a hand starts to move and the moment it returns to a rest position (Kendon 1980; McNeill 1992). Gestures lasting less (resp. more) than 2 seconds were categorized as "short" gestures (n = 10) (resp. "long" gestures; n = 6). Gestures were also divided as follows: 8 of the 16 gestures were defined as "rare" gestures and each was performed by only a few subjects, i.e. less than 17 of our 35 subjects, and 8 other gestures were defined as "common" gestures and were performed by most of our 35 subjects (at least 19 subjects).

Characteristics of the interactional context of gesture production

We recorded the relative positions – visual field used and exposed body side – of both subjects before each dyadic interaction (the last positions in a 2 second time window before the interaction) and during the interaction. Predictability of an interaction was possible by the intentional signalling of the signaller (e.g. gazing at the recipient, gaze alternation, movement towards the recipient).

The emotional contexts of interactions were divided into two categories: positive and negative. This categorization was primarily based on the response of the recipient, but also on the associated global social context as well as the signaller's expressions if necessary. Emotional context was inferred according to (1) the response of the recipient to the signaller's

gesture, that is: apparent change in the recipient's behaviour including communication responses (via gestural, vocal, facial and/or whole-body expressions) or actions (modification of activity – change or stop – , modification of possession of a resource), or no apparent change in the recipient's behaviour; (2) the global social context in which the given interaction occurred: aggression, post-conflict reconciliation and consolation, access to food, object or infant, nursing, grooming, mating, play, and travel; (3) the facial and vocal expressions of the signaller as well as, to a lesser extent, whole-body expressions (e.g. rhythmic movements and piloerection).

Sociodemographic characteristics of the subjects

In addition to the subject's demographic characteristics (age, sex, and zoo), kin and social relationships (affiliation and hierarchy) were considered.

Kinship

Genetically determined kinship data were provided by each zoo. The following three categories of gorilla pairs were considered: (1) "Parent-infant" combining mother-infant and father-infant pairs, (2) "Siblings" combining siblings and half-siblings, and (3) "Unrelated" for pairs of genetically unrelated subjects.

Affiliation

Two indexes of interest have already been used to evaluate relationship quality (Weaver & de Waal 2002); Silk et al. 2013). To remedy disadvantages of the above-mentioned indexes and to better evaluate relationship quality within pairs of individuals (Prieur 2015), we created a Dyadic Affiliation Index (DAI) to quantify affiliation based on the relative frequencies of affiliative and agonistic behaviours within the dyad. This index increases with affinity, starting from 0 in absence of affinity. It is calculated as:

$$DAI_{xy} = \frac{\left(\frac{\sum_{i=1}^{n} \frac{f_{ixy}}{\bar{f}_i}}{n}\right)}{1 + \left(\frac{\sum_{j=1}^{n'} \frac{h_{jxy}}{\bar{h}_j}}{n'}\right)}$$

Where f_{ixy} is the total number of affiliative interactions of the behaviour (i) expressed by x towards y; $\bar{f}_i$ is the mean number of affiliative interactions of the behaviour (i) across all dyads; *n* is the number of affiliative behaviours expressed by x towards y; h_{jxy} is the total number of agonistic interactions of the behaviour (j) expressed by x towards y; $\bar{h}_j$ is the mean number of agonistic interactions of the behaviour (j) across all dyads; *n'* is the number of agonistic behaviours expressed by x towards y. 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" more than 1 (36 dyads).

Affiliative and agonistic behaviours were selected according to Pollick and de Waal (2007). The five following strictly affiliative gestures (gestures expressed only in positive contexts; 4477 interactions) were selected: EMBRACE[18], EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, and TOUCH BODY. All recorded agonistic interactions (1039) were considered. These interactions include mechanically ineffective gestures as KICK and SLAP (Pika et al. 2003) that were not retained hereafter as they did not meet the statistical criteria required for performing binomial tests (see details below in Descriptive statistics), and two mechanically effective social actions: GRAB and PUSH (Pika et al. 2005a).

Hierarchy

Dominance relationships were determined by the analysis of agonistic interactions (Pollick & de Waal 2007) within dyads with clear aggressor and recipient of the threat (Langbein & Puppe 2004).

All recorded agonistic interactions (1039) were taken into account. These interactions were organised into sociometric matrices and analyzed using MatMan 1.1 (Noldus Information Technology, Wageningen, Netherlands). The principles of the methodology used (see Prieur and colleagues, submitted, a, for details) are summarized as follows. MatMan 1.1 assigns a rank from 1 (the most dominant) to N (the most subordinate) to each of the N subjects of one zoo. MatMan did not find a linear hierarchy for La Vallée gorillas. Three categories of hierarchy were considered: "Subordinate", "Intermediate", and "Dominant" (Apenheul: 7 subordinates, 3 intermediates and 4 dominants; Burgers: 4 subordinates, 4 intermediates and 2 dominants; La Vallée: 6 subordinates, 2 intermediates and 3 dominants). The hierarchy of La Vallée gorillas was based on the gorillas' zoo keepers' reports.

[18] Gestures are written in lower capitals

Statistical analysis

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.

Descriptive Statistics

Only data for gestures for which we had at least six subjects who performed at least six times each the given behaviour were considered (Chapelain 2010) to allow subsequent statistical analyses (binominal tests).

Binomial tests on the numbers of responses performed with the left and right hands assessed individual-level biases for each gesture. For each subject, the direction of gestural 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) and the strength of individual hand preference was estimated by the absolute value of the HI (ABSHI) (e.g. Harris & Carlson 1993; Hopkins 1995). Binomial tests assessed population-level biases in the number of lateralized and non-lateralized subjects for each gesture. For each gesture when at least six subjects were lateralized, we assessed population-level biases in the number of right-handers and left-handers using binomial tests. Population-level bias of hand use was evaluated by a one-sample two-sided Student's t-test on the HI values of all subjects when data fitted a normal HI distribution (Shapiro-Wilk normality test) and by a one-sample Wilcoxon signed rank test when data did not fit a normal HI distribution. In addition, we checked the potential effect of the number of data per subject on the HI and ABSHI values using Spearman correlation tests. Pearson correlation tests assessed correlations between the following normally distributed variables: visual field and body side of both signaller and recipient considered before and during an interaction.

Generalized Linear Mixed Model analysis on the multiple influential factors

The possible effect of the interactional context as well as the gesture and sociodemographic characteristics on gestural laterality was assessed using a generalized linear mixed model (GLMM) for binary data (logistic regression) with hand use as the dependent variable (see Table 4 for a descriptive summary of dependent, fixed and random variables).

The fixed variables were the following: position of the recipient in the signaller's visual field during the interaction (noted SVF), position of the signaller in the recipient's visual field during the interaction (noted RVF), emotional context, gesture characteristics

(sensory modality: auditory, tactile or visual; use of a communication tool: with or without object, sharing degree: high or low; duration: short or long) as well as signaller and recipient's social (kinship, hierarchy, dyadic affiliation) and demographic (age, sex, zoo) characteristics. All possible interactions between fixed variables were included at the beginning of the model selection.

In order to avoid pseudoreplication produced by repeated observations (Waller et al. 2013), we considered signallers' and recipients' identities as the random variables. The GLMM analysis was performed using the 'glmer' function ['lme4' package (Bates et al. 2014)]. The model with the lowest Akaike's information criterion (AIC) was retained. Equivariance, independence and normality of model residuals were visually checked using the 'plotresid' function ['RVAideMemoire' package (Hervé 2014)]. The main effects of the best model were tested with type II Wald chi-square tests using the 'Anova' function ['car' package (Fox & Weisberg 2011]. 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 the Tukey's HSD test and calculated between LSmeans ('lsmeans' package).

Results

We recorded 16 801 occurrences of gestures by our 35 subjects during 651 hours observation.

Gestural laterality at the population level

After having applied the statistical criteria required for performing binomial tests (Siegel & Castellan 1988), 16 471 occurrences of gestures were retained for descriptive statistics and related analyses. The mean number of gesture occurrences per subject was 470.600 (min=6, max=1 771; SD=504.343)

To assess gestural laterality at the population level, we analyzed each of the 16 gestures separately. Significantly more subjects were non-lateralized than lateralized for 4 tactile and 1 visual gestures (binomial tests: TOUCH BODY, EMBRACE LATERAL, EMBRACE, EMBRACE VENTRAL/DORSAL: all $P \leq 0.008$; ATTEMPT TO REACH: $P = 0.0009$; details Table 4) and this tended to be moderately true for another tactile gesture EMBRACE HALF (binomial test: $P = 0.070$). On the contrary, more subjects tended to be lateralized than non-lateralized for 2

auditory gestures (binomial tests: BEAT CHEST: $P = 0.064$; SLAP HAND: $P = 0.053$). The average percentage of non-lateralized subjects for all the considered gestures was 62.98% (min=26.32, max=100, SD=26.12).

Significantly more subjects were right-handed than left-handed for the five following gestures: two auditory (CLAP HAND and SLAP HAND), one tactile (PUNCH) and two visual gestures (SHAKE OBJECT and RAISE ARM) (binomial tests: $P \leq 0.006$; details Table 4). Nine gestures presented a significant right-hand bias at the population level (one-sample two-sided t-tests or one-sample Wilcoxon signed rank tests, $P \leq 0.011$; details Table 4) and this tended to be true for two tactile gestures (EMBRACE LATERAL: $P = 0.053$; EMBRACE VENTRAL/DORSAL: $P = 0.092$). The average Mean HI for all gestures was 0.222 (min=-0.021, max=0.530; SD=0.156) and the average Mean ABSHI for all gestures was 0.040 (min=0, max=0.286; SD=0.077).

In addition, the number of data points per subject had no significant effect on the HI values for all the gestures. Only one positive (resp. negative) correlation was found between the number of data points per subject and the ABSHI values for BEAT CHEST (resp. TOUCH BODY) (Spearman correlation tests: BEAT CHEST: N = 19, $r_s = 0.600$, $P = 0.007$; TOUCH BODY: N = 35 $r_s = -0.442$, $P = 0.008$) (detailed in Appendix Table A1).

Factors and their mutual interactions influencing gestural laterality

To investigate the respective influences of interactional context components, gesture characteristics, and sociodemographic characteristics on gestural laterality all the 16 801 gesture performed by our 35 subjects were accounted for in the GLMM analysis. The associated mean number of gesture occurrences per subject was 480.029 (min=11, max=1 771; SD=501.321).

Four different possible combinations of signaller's and recipient's visual fields were recorded during interactions. Their respective percentage of occurrences is given in Figure 1. Whatever the subject (signaller or recipient), the visual fields with which they observed each other were similar in 37.03% of the occurrences (Figs. 1a and 1b) and differed in 62.97% of the occurrences (Figs. 1c and 1d). This translates into a weak negative correlation between the signaller's and the recipient's visual fields during an interaction (Pearson's rank correlation: $r_p = -0.26$, $P < 0.0001$, $n = 16\,794$).

Whatever the subject (signaller or recipient), the visual field in which the partner was located coincided with the body side exposed towards this partner, before interaction

(signaller: Pearson's rank correlation: $r_p = 0.99$, $P < 0.0001$, $n = 16\,789$; recipient: $r_p = 0.99$, $P < 0.0001$, $n = 16\,789$) as well as during the interaction (signaller: $r_p = 0.99$, $P < 0.0001$, $n = 16\,794$; recipient: $r_p = 0.99$, $P < 0.0001$, $n = 16\,794$).

Furthermore, whatever the subject (signaller or recipient), the visual fields in which the partner was located before and during interaction were strongly positively correlated (signaller: $r_p = 0.86$, $P < 0.0001$, $n = 16\,788$; recipient: $r_p = 0.94$, $P < 0.0001$, $n = 16\,788$). These strong positive correlations allowed us to reduce the number of position variables in the GLMM analysis and to retain only the signaller's and recipient's visual fields during an interaction.

Table 5 presents the results of the analysis of deviance corresponding to the best GLMM model. As every fixed variable is involved in significant interactions with other variables, the effect of the fixed variables considered separately must be ignored. Variables for which a significant or trend interaction was found were then considered successively: interactional context variables (signaller visual field, recipient visual field and emotional context), gesture characteristic variables (sensory modality, use of a communication tool, sharing degree, duration) as well as subjects' social (kinship, hierarchy, affiliation) and demographic (age, sex, zoo) variables (Table 5). Results of post-hoc multiple comparisons tests are presented in Appendix Table A2. Table 6 presents a summary of the results. For clarity, significant and trend p-values are mentioned in the text below whereas all p-values are given in Table A2.

Influence of interactional context on gestural laterality

Influence of the position of the recipient in the signaller's visual field during an interaction (SVF). Signallers used more their right hand when the recipient was in their right visual field during an interaction (SVF_R) than in their left visual field (SVF_L) when performing tactile and visual gestures (Fig. 2a) and whatever the emotional context (Fig. 3), use of a communication tool or not (Fig. 4a), gesture duration, kinship and sex of the recipient (Tukey tests: tactile and visual: both $P < 0.0001$; positive and negative emotion: both $P < 0.0001$; with object: $P = 0.024$; without object: $P < 0.0001$; short and long: both $P < 0.0001$; siblings, parent-infant and unrelated pairs: all $P < 0.0001$; female and male recipients: both $P < 0.0001$). No evidence of an influence of SVF on signallers' right-hand use was found for auditory gestures (Fig. 2a).

Influence of the position of the signaller in the recipient's visual field during an interaction (RVF). Signallers used more their right hand when they were located in the right visual field (RVF_R) than in the left visual field (RVF_L) of recipients during an interaction when performing auditory gestures (Fig.2b) and gestures with object (Fig.4b) (Tukey test: auditory: $P = 0.013$; with object: $P = 0.026$). On the contrary signallers used more their right hand when they were located in the left visual field (RVF_L) than in the right visual field (RVF_R) of recipients during an interaction when performing visual gestures (Fig. 2b), gestures without object (Fig. 4b), and for gestures directed towards siblings (visual: $P = 0.002$; without object: $P < 0.0001$; siblings: $P = 0.001$) No evidence of an influence of RVF on signallers' right-hand use was found for tactile gestures (Fig. 2b), parent-infant and unrelated pairs, and whatever gesture duration.

Influence of emotional context. Signallers were more right-handed in negative than in positive emotional contexts when the recipient was in the signaller's right visual field during an interaction (SVF_R) (Fig. 3), and when signallers belonged to the Burgers group (Tukey tests: SVF_R: $P = 0.044$; Burgers: $P = 0.0001$). This tended to be marginally true when they performed highly shared gestures and for gestures directed towards mature adults (highly shared: $P = 0.082$; mature adults: $P = 0.065$). On the contrary signallers from the Vallée group tended to use their right hand moderately more in positive than in negative emotional contexts ($P = 0.069$). No evidence of an influence of emotional context on signaller's right-hand use was found when the recipient was in the signaller's left visual field during an interaction (SVF_L) (Fig. 3), for lowly shared gestures, for gestures directed towards infants, juveniles, adolescents and young adults and for the Apenheul group.

Influence of gesture characteristics on gestural laterality

Influence of gesture sensory modality. Signallers used more their right hand to perform auditory than visual gestures when the recipient was in the signaller's left visual field (SVF_L) (Fig. 2a) and when the signaller was in the recipient's right visual field (RVF_R) (Fig. 2b), for lowly shared gestures, for subordinate signallers (Fig.5), for gestures directed towards low affiliative partners, for adolescent signallers as well as for the Apenheul group (Tukey tests: SVF_L: $P < 0.0001$; RVF_R: $P = 0.004$; lowly shared: $P = 0.029$; subordinate: $P = 0.002$; low affiliative partner: $P = 0.016$; adolescent: $P = 0.0004$; Apenheul: $P < 0.0001$). On the contrary, signallers used more their right hand to perform visual gestures than auditory gestures when the recipient was in the signaller's right visual field (SVF_R) (Fig. 2a) and

when the signallers were infants or juveniles (SVF_R: $P < 0.0001$; infant: $P = 0.0004$: juvenile: $P = 0.012$).

Signallers used more their right hand to perform auditory gestures than tactile gestures when the recipient was in the signaller's left visual field (SVF_L) (Fig. 2a) and when the signaller was in the recipient's right visual field (RVF_R) (Fig. 2b), for gestures directed towards low affiliative partners, and when the signallers were subordinates, adolescents, young adults or females (Fig. 5) or from the Apenheul's group (Tukey test: SVF_L: $P < 0.0001$; RVF_R: $P = 0.0009$; subordinate: $P = 0.001$; low affiliative partner: $P = 0.011$; adolescent: $P = 0.0005$; young adult: $P = 0.0005$; female: $P = 0.010$; Apenheul: $P < 0.0001$). This tended to be moderately true for lowly shared gestures ($P = 0.065$). On the contrary, signallers used their right hand for tactile more than for auditory gestures when the recipient was in their right visual field (SVF_R) (Fig. 2a) and when the signallers were infants (SVF_R: $P < 0.0001$; infant: $P = 0.036$)

No evidence of an influence of gesture sensory modality on signaller's right-hand use was found when the signaller was in the recipient's left visual field (RVF_L) (Fig. 2b), for highly shared gestures, gestures directed towards a strong and a medium affiliative partners as well as when signallers were dominants or intermediates (Fig. 5), mature adults, males or from the Burgers and La Vallée groups.

Influence of the use of a communication tool. Signallers were more right-handed to perform gestures without an object than with an object when the recipient was in their right visual field (SVF_R) (Fig. 4a) and when the signaller was in the recipient's left visual field (RVF_L) (Fig. 4b) (Tukey tests: SVF_R: $P < 0.0001$; RVF_L: $P = 0.009$). On the contrary, signallers were more right-handed to perform gestures with an object than without an object when the recipient was in the signaller's left visual field (SVF_L) (Fig. 4a) and when the signaller was in the recipient's right visual field (RVF_R) (Fig. 4b) (SVF_L: $P < 0.0001$; RVF_R: $P = 0.023$). No evidence of an influence of the use of a communication tool on right-hand use was found whatever the gesture duration.

Influence of gesture sharing degree. Signallers tended to use their right hand to perform lowly shared more than highly shared gestures in positive emotional contexts (Tukey test: positive emotion: $P = 0.062$). No evidence of an influence of gesture sharing degree on right-hand use was found in negative emotional contexts, whatever gesture sensory modality, kinship, age and sex of the signaller and gorilla group.

Influence of gesture duration. Signallers used their right hand more for short than for long gestures when the recipient was in their left visual field (SVF_L) and when the signaller was in the recipient's right visual field (RVF_R), for gestures without object, when signallers were males as well as for gestures directed towards juveniles (Tukey tests: SVF_L: $P < 0.0001$; RVF_R: $P < 0.0001$; without object: $P < 0.0001$; male: $P < 0.0001$; juvenile recipient: $P = 0.0004$). Moreover, this tended to be marginally true for gestures directed towards infants and young adults (infant recipient: $P = 0.096$; young adult recipient: $P = 0.080$). No evidence of an influence of gesture duration on signaller's right-hand use was found when the recipient was in the signaller's right visual field (SVF_R), when the signaller was in the recipient's left visual field (RVF_L), for gestures with object, for female signallers as well as for gestures directed towards adolescents and mature adults.

Influence of sociodemographic characteristics on gestural laterality

Influence of signaller's hierarchical rank. Subordinate signallers used their right hand more than did intermediate signallers for auditory gestures and when they belonged to the La Vallée group (Tukey tests: auditory: $P < 0.0001$; La Vallée: $P < 0.0001$). Moreover, dominant signallers used their right hand more than intermediate signallers when they belonged to the La Vallée group ($P = 0.013$) and this tended to be moderately true for auditory gestures ($P = 0.069$). No evidence of an influence of signaller's hierarchical rank on its right-hand use was found for visual and tactile gestures (Fig.5) as well as when they belonged to the Apenheul or the Burgers group.

Influence of kinship. No evidence of an influence of kinship on signaller's right-hand use was found whatever the position of the recipient in the signaller's visual field during an interaction (SVF_L and SVF_R) and whatever the position of the signaller in the recipient's visual field (RVF_L and RVF_R) and sharing degree.

Influence of affiliation. Signallers were more right-handed when performing visual gestures towards a medium-affiliative partner than towards a low affiliative partner (Tukey test: $P = 0.046$). No evidence of an influence of affiliation on signaller's right-hand use was found for tactile and auditory gestures.

Influence of signaller's age class. Infant signallers were less right-handed than juvenile signallers for auditory gestures and lowly shared gestures (Tukey tests: auditory: $P = 0.030$; lowly shared: $P = 0.045$). Moreover, this tended to be true for gestures directed towards juveniles and young adults (Fig. 6) (juvenile recipient: $P = 0.079$; young adult recipient: $P = 0.067$). Infant signallers were also less right-handed than adolescent signallers for auditory gestures, and whatever the sharing degree of gesture and recipient's age and sex (auditory: $P < 0.0001$; lowly shared and highly shared: $P < 0.0001$; infant recipient: $P = 0.002$; juvenile recipient: $P < 0.0001$; adolescent recipient: $P = 0.003$; young adult recipient: $P < 0.0001$; mature adult recipient: $P = 0.049$; female and male recipient: $P < 0.0001$). Similarly, they were less right-handed than young adult signallers for auditory gestures and whatever the sharing degree of gesture and recipient's sex (auditory: $P < 0.0001$; lowly shared: $P = 0.020$; highly shared: $P = 0.027$; female recipient: $P = 0.005$; male recipient: $P = 0.034$). Furthermore, they were less right-handed than mature adult signallers for auditory gestures, for gestures directed towards young adults (Fig. 6), and towards females (auditory: $P = 0.011$; young adult recipient: $P = 0.038$; female recipient: $P = 0.008$). This tended to be marginally true towards juveniles ($P = 0.084$).

Juvenile signallers were less right-handed than adolescent signallers for auditory gestures as well as for gestures directed towards juveniles (Fig. 6) and whatever the sharing degree of gesture and recipient's sex (Tukey tests: auditory: $P < 0.0001$; juvenile recipient: $P = 0.007$; lowly shared: $P = 0.007$; highly shared: $P = 0.0002$; female recipient: $P = 0.022$; male recipient: $P < 0.0001$). This tended to be moderately true for gestures directed towards adolescents ($P = 0.073$). Juvenile signallers were also less right-handed than young adult signallers for auditory gestures ($P = 0.0002$) and tended to be marginally less right-handed than mature adult signallers for auditory gestures and gestures directed towards females (auditory: $P = 0.094$; female recipient: $P = 0.080$).

No evidence of an influence of signaller's age class on signaller's right-hand use was found for tactile and visual gestures.

Influence of recipient's age class. Infant signallers were more right-handed when performing gestures towards young adults than towards mature adults (Fig. 6) (Tukey test: $P = 0.043$). This tended to be true in negative emotional contexts ($P = 0.070$). No evidence of an influence of recipient's age class on signaller's right-hand use was found when the signaller was a juvenile, an adolescent, a young adult, or a mature adult (Fig. 6) and whatever gesture duration.

Influence of signaller's sex. Female signallers used their right-hand more than did male signallers when performing visual and auditory gestures (Fig. 7), highly shared gestures, long gestures as well as when signallers belonged to the La Vallée group (Tukey tests: visual: $P < 0.0001$; auditory: $P = 0.007$; highly shared: $P < 0.0001$; long: $P = 0.0002$; La Vallée: $P = 0.0002$). This tended to be marginally true for Apenheul signallers ($P = 0.095$). No evidence of an influence of signaller's sex on signaller's right-hand use was found for tactile gestures (Fig. 7), lowly shared gestures, and short gestures or when signallers belonged to the Burgers group.

Influence of recipient's sex. No evidence of an influence of recipient's sex on signaller's right-hand use was found whatever the position of the recipient in the signaller's visual field during an interaction (SVF_L and SVF_R) and the signaller's age class.

Influence of signaller's group (zoo). Signallers belonging to the Apenheul zoo were more right-handed than signallers belonging to the Burgers zoo in positive emotional contexts (Tukey test: $P = 0.012$). Furthermore, they were more right-handed than signallers belonging to the La Vallée zoo in negative emotional contexts, for auditory gestures, lowly shared gestures, when they were subordinates or intermediates or males (negative emotion: $P = 0.031$; auditory: $P < 0.0001$; lowly shared: $P = 0.006$; subordinate: $P = 0.044$; intermediate: $P < 0.0001$; male: $P = 0.015$).

Signallers belonging to the Burgers zoo were more right-handed than La Vallée signallers in negative emotional contexts, for auditory and tactile gestures, lowly shared gestures, when they were intermediates or males (Tukey tests: negative emotion: $P = 0.0008$, auditory: $P = 0.020$; tactile: $P = 0.029$; lowly shared: $P = 0.009$; intermediate: $P < 0.0001$; male: $P = 0.002$).

No evidence of an influence of signaller's group on signaller's right-hand use was found in positive emotional contexts as well as for visual gestures, highly shared gestures, when they were dominants or males.

Discussion

To our knowledge, no study has investigated laterality of intraspecific gestures of gorillas since Shafer's (1987) pioneering study considering a category of undistinguished

types of "any hand motions interpreted as signalling to another gorilla or that were interpreted as solitary gestures" (Shafer 1987, p. 51). The goal of the present study was to improve our understanding of gorillas' gestural laterality by investigating the most frequent gesture types of their natural repertoire. To achieve this goal, two research questions were asked. First, is a gestural laterality bias observed at the population level? Second, which factors influence gestural laterality?

Taking into account laterality on a continuum, 9 of the 16 gestures considered showed a right-hand bias at the population level. Through our multifactorial approach, we evidenced that signallers' gestural laterality was principally modulated by characteristics of the interaction (signaller's and recipient's visual fields, emotional context), of the gestures (sensory modality, use of a communication tool, duration) and signaller's age, sex, group and rank. In particular, signallers used their hand ipsilateral to the recipient for tactile and visual gestures and whatever the emotional context, gesture duration, recipient's sex or the kin relationship between the signaller and the recipient, and whether or not a communication tool was used. The signallers' contralateral hand was not used preferentially in any situation. Moreover, signallers' right-hand use was more pronounced in negative contexts, for short gestures as well as by female signallers. Our results evidenced increase of signallers' right-hand use with age.

Gestural laterality at the population level

As far as we know, the present study is the first to evidence a right-hand bias at the population level for intraspecific gestural communication of gorillas. As chimpanzees in our previous study (Prieur et al. submitted, a), gorillas presented a right-hand bias at the population level for the majority (9 over 16) of the most frequent intraspecific gestures considered. Interestingly, both species presented a right-hand bias at the population level for all these gestures, except CLAP HAND. Our results are in line with previous studies that revealed a right-hand bias at the population level for both inter and intraspecific communication for chimpanzees and baboons (e.g. see reviews Hopkins et al. 2012; Meguerditchian et al. 2013). This right-side predominance of gestures has been evidenced for humans (see review Cochet & Byrne 2013). Taken altogether, the above-mentioned studies as well as the present study support the hypothesis of a predominant involvement of the left cerebral hemisphere in the gestural communication system of humans and certain non-human primates. These findings are in accordance with the theory of the origin of human language proposing that laterality in

gestural communication would represent a prerequisite for the left-hemispheric lateralization of language (Corballis 2002, 2003). To date, the majority of studies devoted to gestural laterality in non-human primates focused on distinct gestures directed towards conspecifics and/or humans (Hopkins et al. 1993; Hopkins et al. 2005b; Fletcher & Weghorst 2005; Fletcher 2006; Meguerditchian & Vauclair 2006; Chapelain 2010; Meguerditchian et al. 2012). To facilitate comparisons with these studies, we focus now on four of the nine gesture types presenting a right-hand bias at the population level. Our results evidenced a right-hand bias at the population level for SLAP HAND and for CLAP HAND, as did Meguerditchian and Vauclair (2006) for captive baboons and Meguerditchian and colleagues (2012) for chimpanzees. However, on the contrary, Fletcher (2006) did not find a hand bias at population level for CLAP (an attention-getting behaviour directed towards humans) for chimpanzees. Our result showing a right-hand preference at the population level for THROW OBJECT is in agreement with Hopkins and colleagues' study of chimpanzees (Hopkins et al. 1993; Hopkins et al. 2005b). We evidenced a right-hand bias at the population level for EMBRACE contrary to Fletcher and Weghorst (2005) for chimpanzees, possibly because they took into account a broader definition of embrace combining not only our EMBRACE but in addition our EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL and EMBRACE HALF, gestures for which we did not find a right-hand bias at the population level. As far as we know, no other author has investigated any of the other five gestures we found to be right-lateralized at the population level. No evidence of hand preference at the population level was found for TOUCH BODY, in agreement with Fletcher and Weghorst (2005) for chimpanzees and Chapelain (2010) for bonobos, as well as Chapelain (2010) for EMBRACE LATERAL and EMBRACE HALF.

We discuss now the influence on gestural laterality of interactional context components, gesture characteristics, and then the subjects' social and demographic characteristics.

Factors and their mutual interactions influencing gestural laterality

Influence of interactional context

Influence of position of recipient in signaller's visual field during an interaction (SVF). Overall, our results showed that signallers were more right-handed when the recipient was in their right (SVF_R) than in their left (SVF_L) visual field during an interaction. Overall, similar results were found for chimpanzees (Prieur et al. submitted, a) except for auditory gestures and gestures with a tool. The greater use of right hand for tactile and visual gestures

for SVF_R than for SVF_L could be explained as follows. By definition (Pika et al. 2003, 2005), tactile gestures imply physical contact with the recipient, thus involving the more likely use of the hand on the side of the recipient (ipsilateral hand). Using the ipsilateral hand during visual gestures would optimize transmission of visual signals. These reasons could also explain the greater right-hand use by gorillas in SVF_R for gestures with an object (all are visual gestures), long gestures (all are either tactile or visual) as well as for gestures without an object and short gestures (categories in which tactile and visual gestures are overrepresented compared to auditory gestures for which an influence of SVF could not be evidenced). When all gestures are considered, tactile (6/16) and visual (6/16) gestures are overrepresented compared to auditory (4/16) gestures, giving them a greater weight on hand preference. This could explain why signallers overall used their right hand more to perform gestures in SVF_R than in SVF_L whatever the emotional context, the recipient's sex and kinship.

Influence of position of signaller in recipient's visual field during an interaction (RVF). Signallers were more right-handed when performing visual gestures and gestures without an object when they were located in the left visual field (RVF_L) than in the right visual field (RVF_R) of recipients during an interaction. Chimpanzees (e.g. Wallez et al. 2012), rhesus macaques (e.g. Hauser 1993), and baboons (e.g. Wallez & Vauclair 2011) as well as humans (e.g. Nicholls et al. 2002) present more pronounced facial expressions of emotions on their left than on their right hemiface. As previously hypothesized for chimpanzees (Prieur et al. submitted, a), more pronounced expressions on the recipient's left hemiface could intensify the signaller's emotional state during an interaction and would thus explain signallers' greater right-hand use in RVF_L for visual gestures and gestures without an object. However, this effect was not apparent for auditory gestures and gestures with an object and this could be due to an additional adverse effect. Indeed, auditory gestures and gestures with an object were used mainly during displays of power in play contexts that include aspects of social assessment (Pellis & Iwanniuk 1999, 2000) or in agonistic contexts (personal observations). This is supported by Schaller (1963) who stressed the importance of auditory gestures in displays by adult male gorillas. We hypothesize that performing powerful displays induces a certain level of stress, potentially exacerbated in RVF_R because the signaller is aware of being on the side of the recipient's hand most used for communication (i.e. right hand) that could be used by the recipient to respond. This stress experienced by the signaller would be

associated with a greater right-hand use (see below discussion of the influence of the signaller's hierarchical rank).

Influence of emotional context. Considering all gestures, signallers were more right-handed in negative than in positive contexts for SVF_R and when they belonged to the Burgers group. We evidenced previously a similar negative context effect on right hand for chimpanzees' common gestures (Prieur et al. submitted, a). These results agree with Rolhf and Ramirez's (2006) review mentioning that "anger" (negative in valence, (e.g. Lazarus 1991) and that often elicits approach motivation (e.g. Berkowitz 1999)) enhanced humans' left-prefrontal brain activity leading to right-hand preference in negative emotional contexts (e.g. Harmon-Jones 2004). This effect was evidenced for SVF_R, possibly because in that case signallers were located 1.74 times more often on the recipient's left-hemiface side (i.e. the most emotionally expressive hemiface that could intensify the signaller's emotional state and consequently could increase its right-hand use). This valence effect could also explain Burgers signallers' greater right-hand use, possibly because of competition for reproduction among Burgers females (a group including two mothers with their offspring and two pregnant mothers). Indeed, harassment of mothers and especially of their infant(s) was relatively frequent and aggressive in this group (personal observations). This type of harassment has already been reported for several species of macaques and baboons (Altmann 1980; Silk 1980, 1983, 1999; Maestripieri 1994a, 1994b; Paul & Kuester 1996).

Influence of gesture characteristics

Influence of gesture sensory modality. Our results showed that signallers overall used their right hand more to perform auditory than tactile and visual gestures. This was the case for SVF_L but the contrary for SVF_R. These differences in right-hand use between SVF_L and SVF_R could be explained by the fact that signallers used more their hand ipsilateral to the recipient to perform tactile and visual gestures whereas their laterality for auditory gestures was not influenced by the position of the recipient in the signaller's visual field. Globally considering both SVF_L and SVF_R, signallers were more right-handed for auditory than for tactile and visual gestures because the LSmeans difference between auditory and tactile gestures (resp. between auditory and visual gestures) for SVF_L was twice (resp. one and a half times) the corresponding absolute value for SVF_R. Chimpanzee signallers however used overall their right hand more to perform visual and tactile than auditory gestures (Prieur et al. submitted, a). Auditory gestures represented a greater part (about one fifth) of the gorillas'

gestural repertoire than of chimpanzees' gestural repertoire (about one-tenth) (Pika et al. 2005a). We hypothesized that this difference may be due to the generally higher interindividual distances kept by gorillas (Klein 1999) compared to chimpanzees (Harcourt 1979); such distances would thus make auditory signals for gorillas particularly relevant to attract more easily the attention of the audience. Because auditory gestures are more common in gorillas, they would be more codified/lateralized in gorillas than in chimpanzees possibly for better social coordination.

Influence of the use of a communication tool in gestures. Gestures with an object involve both communication and manipulation components interfering with each other. We previously evidenced that chimpanzee signallers overall were more right-handed when performing gestures without an object than with an object (Prieur et al. submitted, a). Moreover, we showed that chimpanzees performing gestures with an object were more right-lateralized than when using a tool in non-communication actions (Prieur et al. submitted, b). These studies would indicate that right-side predominance for gestures with an object is intermediate between that for manipulation (manual actions deprived of communication function) and that for gestures without an object (involving only communication components). This hypothesis is probably applicable to other species. The fact that gestures without an object are more right-lateralized than gestures with an object is verified here for gorillas for SVF_R and RVF_L. However, gorillas were more right-handed when performing gestures with an object than gestures without an object for SVF_L and RVF_R. For SVF_L and particularly for interactions involving relative proximity between partners, as we suggested for chimpanzees, signallers performing gestures with an object probably try to prevent the recipient from grabbing the potentially coveted object (personal observation) and/or they may keep their hand close to the recipient free to be used for further potential communication. This would thus explain that signallers preferentially used their hand contralateral to the recipient (i.e. right hand) in SVF_L. For RVF_R, as previously hypothesized (see above discussion about the influence of RVF on right-hand use), producing gestures with an object (i.e. displays of power) would induce a certain level of stress leading to an increased use of signallers' right hand.

Influence of gesture sharing. Overall, we did not evidence an effect of gesture sharing degree on signallers' right-hand use, contrary to chimpanzees (Prieur et al. submitted, a). A reason might be that the categorization of "rare versus common" gestures was less relevant for

gorillas than for chimpanzees. This categorization was based on observed gaps in the distribution of the numbers of subjects (having performed at least six times each a given gesture) between the rare and common gestures. As a matter of fact, the gap separating rare and common gestures for chimpanzees (gap between 13 and 25 subjects) is bigger than the gap for gorillas (gap between 17 and 19 subjects) (see more details in Prieur 2015).

Influence of gesture duration. We showed previously that auditory gestures were overall more right-lateralized than tactile and visual gestures. No evidence of a difference of laterality pattern was found between tactile and visual gestures. Our findings that signallers overall used their right hand more for short than for long gestures could be explained by the difference in terms of involved sensory modality between short gestures (including 1 tactile, 5 visual and 4 auditory gestures) and long gestures (including 5 tactile and 1 visual gestures).

Influence of social characteristics on gestural laterality

Influence of signallers' hierarchical rank. La Vallée subordinate (resp. dominant) signallers were more right-handed than intermediate signallers. Moreover, subordinate (resp. dominant) signallers used (resp. tended to use) their right hand more to perform auditory gestures than did intermediate signallers. These differences may be the consequence of a higher level of psychosocial stress (e.g. competition for food, mates and/or territories) experienced by both subordinates and dominants resulting in a greater right-hand use as hypothesized below.

First, low-ranking social animals usually maintain a higher level of glucorticoïds (i.e. stress hormone) than high-ranking subjects (Creel et al. 2001; Markham et al. 2014). Captivity could exacerbate psychosocial stress (Muller & Wrangham 2004). This stress may be experienced especially by low-ranking captive gorillas for access to food and space. Contrary to chimpanzees (Prieur et al. submitted, a), subordinate gorillas were not more right-handed than dominant gorillas. Because of gorillas' particular social structure, reproduction competition would probably induce some stress among high-ranking gorillas (mostly females) as explained below. Western lowland gorillas live in polygamous harem groups commonly constituted by one silverback, 3 to 4 adult females, and their sexually immature offspring (e.g. Gatti et al. 2004), whereas chimpanzees live in multi-male/multi-female groups characterized by high degree of fission-fusion dynamics (e.g. Aureli et al. 2008). The housing situations at the selected zoos allowed the studied gorillas to live in social structures close to that observed in the wild. Doran-Sheehy and colleagues (2009) showed that wild dominant male western gorillas initiate more copulations with high-ranking females rather than having to distinguish

between pregnant and cycling females. These authors suggested that this mating strategy would allow high-ranking females to divert dominant males' interest away from other females. By doing so, they would reinforce their own dominant status and would potentially delay others' conception. Personal observations suggest that this strategy was adopted particularly by La Vallée dominant females

Second, stress would elicit a right-side bias at the population level for chimpanzees (Prieur al. submitted, a, b), rats (e.g. Alonso et al. 1991; Castellano et al. 1987, 1989) and anoles (Deckel 1998). As Deckel proposed, the right-side bias observed during acute stress could be due to inhibition of the right hemisphere. This assumption is supported by the Rohlfs and Ramirez's (2006) review of reports on humans. They mentioned that stress could induce several neurochemical changes (e.g. increase of dopamine: Bertollucci-D'Angio et al. 1990) causing structural and functional alterations in the right hemisphere (Joseph 1994; Schore 1997; Ben-Schaler et al. 1994). The hypothesized relationship between psychosocial stress and its effect on right-hand use could thus explain our results for the La Vallée group. This effect was also present for auditory gestures but not for tactile and visual gestures, possibly because auditory gestures were mainly performed during power displays (see above discussion of the influence of RVF).

Influence of recipients' hierarchical rank. The iterative model selection leading to the best model showed that recipients' hierarchical rank did not influence signallers' right-hand use. Comparatively, no evidence of an effect of the recipient's hierarchical rank on the signaller's right-hand use was found in chimpanzees (Prieur et al. submitted, a). However, Baraud and colleagues (2009) showed an effect of recipient mangabeys' hierarchical rank on social laterality for approach side and positions (transversal and vertical).

Influence of kinship. We found no evidence of kinship effect on signallers' right-hand use whatever the location of the recipient in the signaller's visual field (SVF) and whatever the location of the signaller in the recipient's visual field (RVF). This absence of kinship effect agrees with our previous findings for chimpanzees (Prieur et al. submitted, a) and with Hopkins and colleagues' (2005b) study of chimpanzees. These collective findings did not evidence an effect of genetic factors on laterality of gestural communication.

Influence of affiliation. Signallers were more right-handed to produce visual gestures towards a medium affiliative partner than towards a low affiliative partner. This result seemed

counter-intuitive considering our previous findings for chimpanzees (Prieur et al. submitted, a) which lead us to hypothesize that psychosocial stress effects (that may increase right-hand use) would be less pronounced when interacting with strong affiliative partners than lower ones.

Influence of individual demographic characteristics on gestural laterality

Influence of signallers' age class. Our results indicated that infant signallers overall used their right hand less than older signallers (i.e. juveniles, adolescents, young and mature adults). Moreover, juvenile signallers overall used their right hand less than older signallers. Thus, signallers' right-hand use appears to increase with age as established by previous studies: for wild chimpanzees for 20 gesture types (pooled data) (Hobaiter & Byrne 2013) and for captive chimpanzees for human-directed FOOD BEG and POINTING (pooled data) (Hopkins & Leavens 1998); for baboons for HAND SLAP directed towards both humans and conspecifics (pooled data) (Meguerditchian & Vauclair 2006). Our previous study (Prieur et al. submitted, a) showed that chimpanzees' right-hand use increased with age until the shift in elderly. Indeed, we evidenced a possible senescence effect on gestural laterality with a decrease of right-hand use by elder chimpanzees, possibly due to physical limitations, lower activity (documented for humans: Hughes et al. 1997; Schut 1998; Ranganathan et al. 2001) and/or lower sociality associated with aging that could decrease the practice-based performance of the right hand that would thus converge towards the performance of the left hand. No such senescence effect was evidenced for our gorillas.

Influence of recipients' age class. Infant signallers were more right-handed when performing gestures towards mature adults than towards young adults. Moreover, this tended to be true for signallers in negative emotional context. For infant signallers interacting with fully mature subjects, maybe this is an effect of psychosocial stress. The same reasoning can probably be applied for signallers in negative contexts.

Influence of signallers' sex. Female signallers overall were more right-handed than male signallers. To our knowledge, only two previous studies detected a sex effect in gestural communication of non-human primates, but with opposite results. Our findings are in accordance with Hopkins and Leavens's (1998) study of chimpanzees, but not with Hopkins and de Wall's (1995) study showing that male bonobos were more right-handed than females. However, other studies did not evidence any sex effect in gestural communication, as for

instance for chimpanzees' gestures directed towards humans (Hopkins et al. 2005a), towards both humans and conspecifics (pooled data) (Hopkins et al. 2005b; Meguerditchian et al. 2010) and towards conspecifics (Prieur et al. submitted, a) and for baboons' gestures directed towards humans (Meguerditchian & Vauclair 2006) and towards both humans and conspecifics (pooled data) (Meguerditchian & Vauclair 2009). Further investigations are required to understand better the influence of sex on primates' gestural laterality and its determinants.

Influence of recipients' sex. No evidence of any effect of recipients' sex on signallers' right-hand use was found. On the contrary, our previous study (Prieur et al. submitted, a) showed that chimpanzee signallers tended to be more right-handed for gestures towards females than towards males. This trend could be due to the fact that most signallers interacting with females were males using common gestures, types of gestures hypothesized to be more strongly codified/lateralized than rare gestures thus facilitating social interactions. This is probably beneficial in terms of fitness (e.g. reproductive success) for chimpanzee males' gestures towards females living in multi-male/multi-female groups, but less necessary for western lowland gorillas living in polygamous harem groups.

Influence of signallers' group (zoo). Apenheul and Burgers signallers overall were more right-handed than La Vallée signallers. Moreover, Apenheul signallers were more right-handed than Burgers signallers in positive contexts. These differences between groups/zoos may be the consequence of social pressures hypothesized to explain differences between social groups in laterality in communication functions (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009).

For chimpanzees, however, we did not evidence such clear differences between groups/zoos: differences in signallers' right-hand use were found between two groups only for auditory gestures. Other studies did not find any group effect on hand preference for gestures directed towards humans (chimpanzees: Hopkins et al. 2005a; Meguerditchian et al. 2012) or towards both humans and conspecifics (pooled data) (chimpanzees: Hopkins et al. 2005b; baboons: Meguerditchian et al. 2011).

The goal of our study was to explore in detail gorillas' gestural laterality in intraspecific communication: first by considering separately the most frequent gestures of their communication repertoire, and second by examining how multiple potential influential

factors would modulate their gestural laterality. We concluded that our gorillas were right-handed at the population level for the majority of intraspecific gestures analyzed. In addition, their gestural laterality was influenced by several factors and their mutual intertwinement. More precisely, signallers predominantly used their hand ipsilateral to the recipient for tactile and visual gestures whatever the emotional context, gesture duration, recipient's sex or the kin relationship between the signaller and the recipient, and whether or not a communication tool was used. Furthermore, signallers' right-hand use was more pronounced in negative contexts, for short gestures and when signallers were females. It increased with age. Our findings overall support Ghirlanda and colleagues' (2009) model postulating that population-level bias could be explained by an evolutionary stable strategy based on intraspecific interactions. Our findings provide additional support to a growing literature evidencing predominance of right-hand use in gestural communication by some non-human primates and suggesting that gestural laterality would be a prerequisite for the language left-cerebral specialization. Preliminary comparisons between our findings for gorillas and our previous findings for chimpanzees suggest that social structures and dynamics would explain certain differences in gestural laterality between the two species. Additional studies applying a comprehensive approach to other gorilla and chimpanzee groups as well as to other species and considering multiple potentially modulating factors and real-life social-ecological contexts are mandatory to understand better the evolutionary origins of human handedness and language.

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Table notes

Table 1. F: Female; M: Male

Table 2. Gestures are grouped by sensory modality (4 auditory, 6 tactile and 6 visual gestures) and presented by alphabetic order. Gestures marked with * are followed by descriptions inspired from the mentioned reference(s); they are labelled differently because details based on personal observations have been added.

Table 3. Gestures are grouped by sensory modality and classified by increasing HI values. *N*: number of subjects who performed at least 6 times each the given gesture; Data points analyzed: number of data points associated with the N subjects; Non-lat: Number of non-lateralized subjects; B test Lat. vs. Non-lat.: p-value of the binomial test on the numbers of lateralized versus non-lateralized subjects; LH: number of left-handed subjects; RH: number of right-handed subjects; B test LH vs. RH: p-value of the binomial test on the numbers of left-handed versus right-handed subjects; -: insufficient number of lateralized subjects for a test; Mean HI: Mean Handedness Index score of N subjects, the sign indicates the direction of the gestural bias (negative: left-hand bias, positive: right-hand bias); t-test: t-value and p-value of the t-test performed only for normally distributed HI values of N subjects; Wilcoxon test: W-value and p-value of the Wilcoxon test performed only when normality of HI data was not verified; Mean ABSHI: Mean Absolute value of Handedness Index score of N subjects. Significant results are in bold.

Table 4. L: Left; R: Right; F: Female; M: Male

Table 5. 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 in bold.

Table 6. L: Left; R: Right; Dom: Dominant; A>B: means "signallers used their right hand more when A than when B"; X: statistical evidence

Table A1. HI: Gestures are grouped by sensory modality (4 auditory, 6 tactile and 6 visual gestures) and presented by alphabetic order. Handedness Index; ABSHI: Mean Absolute

value of Handedness Index; rs: Spearman's rho; *P*: Spearman's p-value; *N*: number of subjects who performed the considered gesture at least 6 times each. Significant results are in bold.

Table A2. L: Left; R: Right; F: Female; M: Male; Inf.: Infant; Juv.: Juvenile; Ado.: Adolescent; Y.adu.: Young adult; M.adu.: Mature adult; P: Positive; N: Negative; contrast: difference between LSmeans; estimate: results 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 1. Individual characteristics of the study sample

Name	Age	Sex	Zoo
Mature adult (over 20 years)			
Virunga	42	F	Vallée des Singes
Gaja	40	F	Vallée des Singes
Lobo	39	F	Apenheul
Mintha	38	F	Apenheul
Mandji	37	F	Apenheul
Yaoundé	28	M	Vallée des Singes
Moséka	28	F	Vallée des Singes
Bauwi	24	M	Burgers' zoo
Young adult (12–20 years)			
N'Gayla	20	F	Burgers' zoo
Makoua	19	F	Burgers' zoo
Jambo	18	M	Apenheul
Shatilla	16	F	Burgers' zoo
Kisiwa	15	F	Apenheul
Nimba	14	F	Burgers' zoo
Likale	12	M	Burgers' zoo
Adolescent (7–11 years)			
Nemsi	11	F	Apenheul
Gyasi	10	F	Apenheul
N'Aika	8	F	Burgers' zoo
Shailâ	7	F	Burgers' zoo
Sango	7	M	Vallée des Singes
Lomako	7	M	Vallée des Singes
Juvenile (4–6 years)			
Miliki	6	F	Vallée des Singes
N'Akouh	4	M	Burgers' zoo
N'Washi	4	F	Burgers' zoo
Wimbe	4	M	Apenheul
Mapasa	4	M	Apenheul
Touni	4	F	Vallée des Singes
Infant (0–3 years)			
Mfungaji	3	F	Apenheul
Djomo	3	M	Vallée des Singes
Mzungu	1	M	Apenheul
Chama	1	F	Apenheul
Tayari	1	F	Apenheul
Iriki	1	F	Apenheul
Wéfa	0,9	F	Vallée des Singes
Mawété	0,5	M	Vallée des Singes

Table 2. Gestural repertoire and detailed description

Gesture	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 arm of signaller is stretched and raised up to about head level with palm facing downwards or placed lightly on the recipient's body	Roth (1995)
EMBRACE HALF	Subject puts one arm around another subject while walking	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)
PUNCH *	Any sort of contact made with fist/wrist or fingers of one hand with another subject, without appreciable force, but the actual contact is more forceful than a simple laying of the hand on another's body	Pollick & de Waal (2007)
TOUCH BODY *	Gentle and brief (<5 sec) contact of the recipient's body (except genitals) with one hand or arm	Pika et al. (2003, 2005)
ATTEMPT TO REACH *	Subject briefly extends hand (with fingers slightly flexed with palm up or down) towards another subject, as an attempt to touch/catch it	
DRAG OBJECT	Subject pulls an object (e.g. branch) on the ground with one hand towards another subject	Nishida et al. (1999, 2010)
PUT OBJECT ON HEAD/BACK *	Subject places an object (e.g. branch) on its head/back with one hand	Nishida et al. (2010)
RAISE ARM	Subject lifts one out-stretched arm (all or only forearm) overhead in a quick jerky movement with fingers slightly flexed	Plooij (1984)
SHAKE OBJECT *	An object (e.g. branch) is moved back and forth with quick jerky movements of one arm, slightly or vigorously, while the subject is sitting or standing	Kano (1992, 1998)
THROW OBJECT *	Subject sends an object (e.g. branch) through the air with one hand towards another subject	Hohmann & Fruth (2003a, b)

Table 3 Characteristics, descriptive statistics and analyses of each gesture

Gesture	Sensory modality	Object manipulation	Duration	Sharing degree	N analyzed	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
BEAT CHEST	Auditory	No	Short	High	19	1930	5	0.064	4	10	0.180	0.155	0.351	t=0.155	*P*=0.152	0.400
BEAT BODY	Auditory	No	Short	Low	12	258	9	0.146	0	3	-	0.193	0.759	t=0.193	*P*=0.154	0.396
CLAP HAND	Auditory	No	Short	Low	17	788	5	0.144	1	11	**0.006**	0.508	**0.003**	W=141	***P*=0.001**	0.678
SLAP HAND	Auditory	No	Short	High	22	1710	6	0.053	0	16	**0**	0.530	0.611	t=0.530	***P*<0.0001**	0.530
EMBRACE HALF	Tactile	No	Long	Low	8	119	7	0.070	1	0	-	-0.021	0.461	t=-0.021	*P*=0.885	0.271
TOUCH BODY	Tactile	No	Long	High	35	2827	29	**0.0001**	2	4	0.688	0.041	**0.020**	W=349	*P*=0.588	0.233
EMBRACE LATERAL	Tactile	No	Long	High	21	1020	19	**0.0002**	1	1	-	0.106	0.628	t=0.106	*P*=0.053	0.191
EMBRACE	Tactile	No	Long	Low	15	325	13	**0.007**	0	2	-	0.169	0.371	t=0.169	***P*=0.011**	0.204
EMBRACE VENTRAL/DORSAL	Tactile	No	Long	Low	8	81	8	**0.008**	0	0	-	0.210	0.413	t=0.210	*P*=0.092	0.310
PUNCH	Tactile	No	Short	High	28	2056	14	1	1	13	**0.002**	0.284	0.588	t=0.284	***P*<0.0001**	0.306
DRAG OBJECT	Visual	Yes	Long	Low	14	431	8	0.791	1	5	0.219	0.045	0.495	t=0.045	*P*=0.745	0.411
THROW OBJECT	Visual	Yes	Short	Low	15	683	11	0.119	0	4	-	0.148	0.786	t=0.148	***P*=0.004**	0.179
ATTEMPT TO REACH	Visual	No	Short	High	22	560	19	**0.0009**	0	3	-	0.254	0.097	t=0.254	***P*=0.0003**	0.317
PUT OBJECT ON HEAD/BACK	Visual	Yes	Short	Low	16	1022	11	0.210	0	5	-	0.258	0.461	t=0.257	***P*=0.0002**	0.266
SHAKE OBJECT	Visual	Yes	Short	High	20	1539	7	0.263	0	13	**0.0002**	0.299	0.757	t=0.299	***P*<0.0001**	0.328
RAISE ARM	Visual	No	Short	High	19	1122	6	0.167	1	12	**0.003**	0.380	0.948	t=0.380	***P*<0.0001**	0.410

Table 4. Generalized linear mixed model with dependent, fixed and random variables, their type and associated levels

Name	Type
Dependent variable	
Hand use	Dichotomous (L/R)
Fixed variables	
Position of recipient in Signaller's Visual Field during interaction (SVF)	Dichotomous (L/R)
Position of signaller in Recipient's Visual Field during interaction (RVF)	Dichotomous (L/R)
Emotional context of interaction	Dichotomous (Negative/Positive)
Signaller's sex	Dichotomous (F/M)
Signaller's age class	Ordinal (Infant/Juvenile/Adolescent/Young adult/Mature adult)
Recipient's sex	Dichotomous (F/M)
Recipient's age class	Ordinal (Infant/Juvenile/Adolescent/Young adult/Mature adult)
Zoo	Nominal (Apenheul/Burgers/Vallee)
Signaller's hierarchical rank	Ordinal (Dominant/Intermediate/Subordinate)
Recipient's hierarchical rank	Ordinal (Dominant/Intermediate/Subordinate)
Kinship	Nominal (Parent-infant/Siblings/Unrelated)
Affiliation	Ordinal (Low/Medium/Strong)
Sensory modality	Nominal (Auditory/Tactile/Visual)
Communication tool	Dichotomous (Yes/No)
Duration	Dichotomous (Short/Long)
Sharing degree	Dichotomous (Low/High)
Random variables	
Signaller's identity	Nominal
Recipient's identity	Nominal

Table 5. Analysis of deviance table (Type II Wald chi-square tests)

Fixed variables:	χ^2	Df	*P*
Signaller Visual Field during interaction (SVF)	1290.403	1	<2.2e-16
Recipient Visual Field during interaction (RVF)	54.927	1	1.251e-13
Emotion	5.785	1	0.016
Gesture sensory modality	22.131	2	1.564e-05
Object manipulation gesture	5.447	1	0.020
Gesture duration	37.813	1	7.785e-10
Sharing degree of gesture	10.193	1	0.001
Signaller's hierarchical rank	39.636	2	2.472e-09
Kinship	0.332	2	0.847
Affiliation	3.319	2	0.190
Signaller's age class	46.900	4	1.600e-09
Recipient's age class	4.858	4	0.302
Signaller's sex	25.513	1	4.395e-07
Recipient's sex	7.329	1	0.007
Zoo	36.538	2	1.164e-08
Interactions:			
Context			
SVF × Emotion	18.784	1	**1.464e-05**
Context × Gestural characteristics			
SVF × Gesture sensory modality	530.547	2	**<2.2e-16**
RVF × Gesture sensory modality	40.157	2	**1.905e-09**
SVF × Object manipulation gesture	195.191	1	**<2.2e-16**
RVF × Object manipulation gesture	30.570	1	**3.220e-08**
SVF × Gesture duration	11.288	1	**0.0008**
RVF × Gesture duration	7.276	1	**0.007**
Emotion × Sharing degree of gesture	5.898	1	**0.015**
Context × Social characteristics			
SVF × Kinship	11.623	2	**0.003**
RVF × Kinship	11.916	2	**0.003**
Context × Demographic characteristics			
SVF × Recipient's sex	4.738	1	**0.030**
Emotion × Recipient's age class	11.283	4	**0.023**
Emotion × Recipient's sex	4.478	1	**0.034**
Emotion × Zoo	21.807	2	**1.840e-05**
Gestural characteristics			
Gesture sensory modality × Sharing degree of gesture	28.219	2	**7.452e-07**
Object manipulation gesture × Gesture duration	4.227	1	**0.040**
Gestural characteristics × Social characteristics			
Gesture sensory modality × Signaller's hierarchical rank	54.282	4	**4.594e-11**
Gesture sensory modality × Affiliation	20.181	4	**0.0005**
Sharing degree of gesture × Kinship	7.743	2	**0.021**
Gestural characteristics × Demographic characteristics			
Gesture duration × Signaller's sex	6.714	1	**0.010**
Gesture duration × Recipient's age class	14.637	4	**0.006**
Gesture sensory modality × Signaller's age class	80.768	8	**3.424e-14**
Gesture sensory modality × Signaller's sex	21.492	2	**2.154e-05**
Gesture sensory modality × Zoo	139.551	4	**<2.2e-16**
Object manipulation gesture × Recipient's sex	5.647	1	**0.017**
Sharing degree of gesture × Signaller's age class	9.192	4	0.056
Sharing degree of gesture × Signaller's sex	13.878	1	**0.0002**
Sharing degree of gesture × Zoo	16.629	2	**0.0002**
Social characteristics × Demographic characteristics			
Signaller's hierarchical rank × Zoo	78.466	4	**3.680e-16**
Demographic characteristics			
Signaller's age class × Recipient's age class	33.389	16	**0.007**
Signaller's age class × Recipient's sex	9.017	4	0.061
Signaller's sex × Zoo	13.616	2	**0.001**

Table 6. Generalized linear mixed model: summary of results

		Influence of interactional context					
		Position of recipient in Signaller's Visual Field during interaction (SVF)		*Position of signaller in Recipient's Visual Field during interaction (RVF)*		*Emotional context*	
		SVF_R>SFV_L	SVF_R<SFV_L	RVF_L>RFV_R	RVF_L<RFV_R	N>P	N<P
Position of recipient in Signaller's Visual Field during interaction (SVF)	SVF_R					X	
	SVF_L						
Position of signaller in Recipient's Visual Field during interaction (RVF)	RVF_R						
	RVF_L						
Emotional context	Positive (P)	X					
	Negative (N)	X					
Gestures	Tactile (T)	X					
	Visual (V)	X		X			
	Auditory (A)				X		
	With object	X			X		
	Without object	X		X			
	Short (Sh)	X					
	Long (Lo)	X					
	Rare						
	Common						
Kinship	Parent-infant	X					
	Siblings	X		X			
	Unrelated	X					
Signaller's hierarchical rank	Subordinate (Sub)						
	Intermediate (Int)						
Affiliation	Low						
Signaller's age class	Infant (I)						
	Juvenile (J)						
	Adolescent (Ad)						
	Young Adult (YA)						
Signaller's sex	Male (M)						
	Female (F)						
Recipent's age class	Infant (I)						
	Juvenile (J)						
	Adolescent (Ad)						
	Young Adult (YA)						
	Mature Adult (MA)						
Recipient's sex	Male (M)	X					
	Female (F)	X					
Zoo	Burgers (B)					X	
	Apenheul (Ap)						
	La Vallée (LV)						

Table 6. continued

		Influence of gesture characteristics							
		Sensory modality				*Communication tool*		*Duration*	
		A>V	A<V	A>T	A<T	Without >With object	Without< With object	Sh>Lo	Sh<Lo
Position of recipient in Signaller's Visual Field during interaction (SVF)	SVF_R		X		X	X			
	SVF_L	X		X			X	X	
Position of signaller in Recipient's Visual Field during interaction (RVF)	RVF_R	X		X			X	X	
	RVF_L					X			
Emotional context	Positive (P)								
	Negative (N)								
Gestures	Tactile (T)								
	Visual (V)								
	Auditory (A)								
	With object								
	Without object							X	
	Short (Sh)								
	Long (Lo)								
	Rare	X							
	Common								
Kinship	Parent-infant								
	Siblings								
	Unrelated								
Signaller's hierarchical rank	Subordinate (Sub)	X		X					
	Intermediate (Int)								
Affiliation	Low	X		X					
Signaller's age class	Infant (I)		X		X				
	Juvenile (J)		X						
	Adolescent (Ad)	X		X					
	Young Adult (YA)			X					
Signaller's sex	Male (M)							X	
	Female (F)			X					
Recipent's age class	Infant (I)								
	Juvenile (J)							X	
	Adolescent (Ad)								
	Young Adult (YA)								
	Mature Adult (MA)								
Recipient's sex	Male (M)								
	Female (F)								
Zoo	Burgers (B)								
	Apenheul (Ap)	X		X					
	La Vallée (LV)								

Table 6. continued

		Influence of individual social characteristics			**Influence of individual demographic characteristics**												
		Signaller's hierarchical rank		*Affiliation*	*Signaller's age class*						*Recipient's age class*	*Signaller's sex*		*Signaller's group (zoo)*		
		Sub>Int	Dom>Int	Medium>Low	I<J	I<Ad	I<YA	I<MA	J<Ad	J<YA	YA>MA	F>M	F<M	Ap>B	Ap>LV	B>LV
Position of recipient in Signaller's Visual Field during interaction (SVF)	SVF_R															
	SVF_L															
Position of signaller in Recipient's Visual Field during interaction (RVF)	RVF_R															
	RVF_L															
Emotional context	Positive (P)													X		
	Negative (N)														X	X
Gestures	Tactile (T)															X
	Visual (V)			X								X				
	Auditory (A)	X			X	X	X	X	X	X		X			X	X
	With object															
	Without object															
	Short (Sh)															
	Long (Lo)											X				
	Rare				X	X	X		X						X	X
	Common					X	X		X			X				
Kinship	Parent-infant															
	Siblings															
	Unrelated															
Signaller's hierarchical rank	Subordinate (Sub)														X	
	Intermediate (Int)														X	X
Affiliation	Low															
Signaller's age class	Infant (I)										X					
	Juvenile (J)															
	Adolescent (Ad)															
	Young Adult (YA)															
Signaller's sex	Male (M)														X	X
	Female (F)															
Recipent's age class	Infant (I)					X										
	Juvenile (J)					X			X							
	Adolescent (Ad)					X										
	Young Adult (YA)					X		X								
	Mature Adult (MA)					X										
Recipient's sex	Male (M)					X	X		X							
	Female (F)					X	X	X	X							
Zoo	Burgers (B)															
	Apenheul (Ap)															
	La Vallée (LV)	X	X									X				

Table A1. Effect of the number of data points for each subject on laterality for each gesture

Gesture	Spearman correlation test between number of data points and HI values			Spearman correlation test between number of data points and ABSHI values		
BEAT CHEST	rs = -0.092	*P* = 0.708	*N* = 19	rs = 0.600	***P* = 0.007**	*N* = 19
BEAT BODY	rs = 0.032	*P* = 0.921	*N* = 12	rs = -0.311	*P* = 0.325	*N* = 12
CLAP HAND	rs = 0.348	*P* = 0.172	*N* = 17	rs = 0.402	*P* = 0.110	*N* = 17
SLAP HAND	rs = -0.257	*P* = 0.249	*N* = 22	rs = -0.257	*P* = 0.249	*N* = 22
EMBRACE	rs = 0.085	*P* = 0.764	*N* = 15	rs = 0.019	*P* = 0.947	*N* = 15
EMBRACE LATERAL	rs = -0.198	*P* = 0.390	*N* = 21	rs = -0.293	*P* = 0.197	*N* = 21
EMBRACE HALF	rs = -0.446	*P* = 0.268	*N* = 8	rs = -0.273	*P* = 0.513	*N* = 8
EMBRACE VENTRAL/DORSAL	rs = 0.002	*P* = 0.997	*N* = 8	rs = -0.025	*P* = 0.953	*N* = 8
PUNCH	rs = -0.173	*P* = 0.379	*N* = 28	rs = -0.210	*P* = 0.285	*N* = 28
TOUCH BODY	rs = -0.083	*P* = 0.634	*N* = 35	rs = -0.442	***P* = 0.008**	*N* = 35
DRAG OBJECT	rs = 0.235	*P* = 0.419	*N* = 14	rs = -0.324	*P* = 0.258	*N* = 14
PUT OBJECT ON HEAD/BACK	rs = -0.064	*P* = 0.813	*N* = 16	rs = -0.102	*P* = 0.707	*N* = 16
SHAKE OBJECT	rs = -0.100	*P* = 0.676	*N* = 20	rs = -0.248	*P* = 0.292	*N* = 20
THROW OBJECT	rs = -0.029	*P* = 0.917	*N* = 15	rs = 0.140	*P* = 0.618	*N* = 15
RAISE ARM	rs = -0.424	*P* = 0.070	*N* = 19	rs = -0.447	*P* = 0.055	*N* = 19
ATTEMPT TO REACH	rs = -0.375	*P* = 0.086	*N* = 22	rs = -0.258	*P* = 0.247	*N* = 22

Table A2. Results of post-hoc multiple comparisons tests

SVF × Emotion						
contrast			estimate	SE	z.ratio	*P*
R,N	-	L,N	1.939	0.195	9.930	**<0.0001**
R,N	-	R,P	0.743	0.284	2.617	**0.044**
L,N	-	L,P	-0.104	0.268	-0.388	0.980
R,P	-	L,P	1.092	0.069	15.795	**<0.0001**
SVF × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
R,Auditory	-	L,Auditory	-0.145	0.147	-0.985	0.923
R,Auditory	-	R,Tactile	-0.881	0.174	-5.064	**<0.0001**
R,Auditory	-	R,Visual	-1.003	0.183	-5.468	**<0.0001**
L,Auditory	-	L,Tactile	1.626	0.164	9.889	**<0.0001**
L,Auditory	-	L,Visual	1.471	0.160	9.182	**<0.0001**
R,Tactile	-	L,Tactile	2.363	0.142	16.615	**<0.0001**
R,Tactile	-	R,Visual	-0.122	0.197	-0.618	0.990
L,Tactile	-	L,Visual	-0.155	0.168	-0.922	0.941
R,Visual	-	L,Visual	2.329	0.131	17.767	**<0.0001**
RVF × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
R,Auditory	-	L,Auditory	0.378	0.115	3.285	**0.013**
R,Auditory	-	R,Tactile	0.674	0.169	3.997	**0.001**
R,Auditory	-	R,Visual	0.606	0.169	3.593	**0.004**
L,Auditory	-	L,Tactile	0.071	0.169	0.421	0.998
L,Auditory	-	L,Visual	-0.139	0.172	-0.806	0.966
R,Tactile	-	L,Tactile	-0.224	0.108	-2.083	0.296
R,Tactile	-	R,Visual	-0.067	0.179	-0.377	0.999
L,Tactile	-	L,Visual	-0.210	0.183	-1.146	0.862
R,Visual	-	L,Visual	-0.367	0.097	-3.772	**0.002**
SVF × Object manipulation						
contrast			estimate	SE	z.ratio	*P*
R,No	-	L,No	2.604	0.115	22.659	**<0.0001**
R,No	-	R,Yes	1.114	0.151	7.383	**<0.0001**
L,No	-	L,Yes	-1.063	0.125	-8.474	**<0.0001**
R,Yes	-	L,Yes	0.427	0.151	2.827	**0.024**
RVF × Object manipulation						
contrast			estimate	SE	z.ratio	*P*
R,No	-	L,No	-0.478	0.073	-6.532	**<0.0001**
R,No	-	R,Yes	-0.382	0.134	-2.848	**0.023**
L,No	-	L,Yes	0.433	0.139	3.119	**0.010**
R,Yes	-	L,Yes	0.336	0.120	2.808	**0.026**
SVF × Duration						
contrast			estimate	SE	z.ratio	*P*
R,Long	-	L,Long	1.723	0.140	12.344	**<0.0001**
R,Long	-	R,Short	-0.125	0.103	-1.207	0.622
L,Long	-	L,Short	-0.539	0.097	-5.584	**<0.0001**
R,Short	-	L,Short	1.308	0.109	11.967	**<0.0001**
RVF × Duration						
contrast			estimate	SE	z.ratio	*P*
R,Long	-	L,Long	-0.233	0.105	-2.222	0.117
R,Long	-	R,Short	-0.495	0.098	-5.033	**<0.0001**
L,Long	-	L,Short	-0.169	0.100	-1.693	0.328
R,Short	-	L,Short	0.092	0.071	1.285	0.573
Sharing degree × Emotion						
contrast			estimate	SE	z.ratio	*P*
Low,N	-	High,N	-0.203	0.255	-0.798	0.856
Low,N	-	Low,P	0.041	0.310	0.132	0.999
High,N	-	High,P	0.598	0.252	2.373	0.082
Low,P	-	High,P	0.354	0.142	2.486	0.062

Table A2. continued

Kinship × SVF						
contrast			estimate	SE	z.ratio	*P*
Parent-infant,R	-	Siblings,R	0.147	0.161	0.917	0.942
Parent-infant,R	-	Unrelated,R	0.139	0.138	1.007	0.916
Parent-infant,R	-	Parent-infant,L	1.804	0.156	11.559	**<0.0001**
Siblings,R	-	Unrelated,R	-0.009	0.145	-0.061	1.000
Siblings,R	-	Siblings,L	1.374	0.118	11.654	**<0.0001**
Unrelated,R	-	Unrelated,L	1.368	0.122	11.213	**<0.0001**
Parent-infant,L	-	Siblings,L	-0.282	0.156	-1.813	0.457
Parent-infant,L	-	Unrelated,L	-0.297	0.129	-2.298	0.195
Siblings,L	-	Unrelated,L	-0.015	0.142	-0.105	1.000
Kinship × RVF						
contrast			estimate	SE	z.ratio	*P*
Parent-infant,R	-	Siblings,R	0.054	0.160	0.336	0.999
Parent-infant,R	-	Unrelated,R	-0.121	0.133	-0.911	0.944
Parent-infant,R	-	Parent-infant,L	-0.018	0.123	-0.146	1.000
Siblings,R	-	Unrelated,R	-0.175	0.142	-1.227	0.824
Siblings,R	-	Siblings,L	-0.260	0.066	-3.960	**0.001**
Unrelated,R	-	Unrelated,L	0.065	0.101	0.645	0.988
Parent-infant,L	-	Siblings,L	-0.188	0.157	-1.204	0.835
Parent-infant,L	-	Unrelated,L	-0.038	0.132	-0.284	1.000
Siblings,L	-	Unrelated,L	0.151	0.143	1.056	0.899
SVF × Recipient's sex						
contrast			estimate	SE	z.ratio	*P*
R,F	-	L,F	1.600	0.108	14.852	**<0.0001**
R,F	-	R,M	-0.322	0.248	-1.295	0.566
L,F	-	L,M	-0.491	0.245	-2.000	0.188
R,M	-	L,M	1.431	0.123	11.588	**<0.0001**
Recipient's age class × Emotion						
contrast			estimate	SE	z.ratio	*P*
Ado.,N	-	Inf.,N	-1.228	0.899	-1.367	0.937
Ado.,N	-	Juv.,N	-0.216	0.567	-0.381	1.000
Ado.,N	-	M.adu.,N	-1.709	0.624	-2.741	0.158
Ado.,N	-	Y.adu.,N	0.394	0.310	1.271	0.960
Ado.,N	-	Ado.,P	-0.411	0.395	-1.039	0.990
Inf.,N	-	Juv.,N	1.012	0.930	1.089	0.986
Inf.,N	-	M.adu.,N	-0.481	0.984	-0.489	1.000
Inf.,N	-	Y.adu.,N	1.623	0.961	1.689	0.802
Inf.,N	-	Inf.,P	1.160	0.869	1.335	0.946
Juv.,N	-	M.adu.,N	-1.493	0.748	-1.995	0.602
Juv.,N	-	Y.adu.,N	0.610	0.615	0.992	0.993
Juv.,N	-	Juv.,P	-0.103	0.510	-0.202	1.000
M.adu.,N	-	Y.adu.,N	2.104	0.690	3.048	0.070
M.adu.,N	-	M.adu.,P	1.532	0.498	3.077	0.065
Y.adu.,N	-	Y.adu.,P	-0.582	0.387	-1.503	0.892
Ado.,P	-	Inf.,P	0.342	0.187	1.828	0.718
Ado.,P	-	Juv.,P	0.092	0.181	0.506	1.000
Ado.,P	-	M.adu.,P	0.233	0.329	0.707	1.000
Ado.,P	-	Y.adu.,P	0.223	0.187	1.191	0.974
Inf.,P	-	Juv.,P	-0.251	0.180	-1.392	0.930
Inf.,P	-	M.adu.,P	-0.109	0.325	-0.336	1.000
Inf.,P	-	Y.adu.,P	-0.119	0.215	-0.555	1.000
Juv.,P	-	M.adu.,P	0.141	0.332	0.425	1.000
Juv.,P	-	Y.adu.,P	0.131	0.169	0.775	0.999
M.adu.,P	-	Y.adu.,P	-0.010	0.333	-0.030	1.000

Table A2. continued

Emotion × Recipient's sex						
contrast			estimate	SE	z.ratio	*P*
N,F	-	P,F	-0.216	0.287	-0.753	0.875
N,F	-	N,M	-0.942	0.487	-1.936	0.213
P,F	-	P,M	0.130	0.101	1.281	0.575
N,M	-	P,M	0.855	0.423	2.023	0.180
Emotion × Zoo						
contrast			estimate	SE	z.ratio	*P*
N,Apenheul	-	P,Apenheul	0.354	0.410	0.862	0.955
N,Apenheul	-	N,Burgers	-1.008	0.485	-2.077	0.299
N,Apenheul	-	N,Vallee	1.590	0.527	3.014	**0.031**
P,Apenheul	-	P,Burgers	0.452	0.136	3.316	**0.012**
P,Apenheul	-	P,Vallee	0.027	0.206	0.129	1.000
N,Burgers	-	P,Burgers	1.814	0.400	4.539	**0.0001**
N,Burgers	-	N,Vallee	2.598	0.645	4.030	**0.001**
P,Burgers	-	P,Vallee	-0.425	0.214	-1.993	0.346
N,Vallee	-	P,Vallee	-1.209	0.443	-2.731	0.069
Sharing degree × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
Low,Auditory	-	High,Auditory	0.409	0.187	2.190	0.243
Low,Auditory	-	Low,Tactile	0.551	0.200	2.755	0.065
Low,Auditory	-	Low,Visual	0.556	0.183	3.040	**0.029**
High,Auditory	-	High,Tactile	0.194	0.143	1.359	0.752
High,Auditory	-	High,Visual	-0.088	0.146	-0.604	0.991
Low,Tactile	-	High,Tactile	0.052	0.202	0.256	1.000
Low,Tactile	-	Low,Visual	0.005	0.203	0.025	1.000
High,Tactile	-	High,Visual	-0.282	0.145	-1.944	0.375
Low,Visual	-	High,Visual	-0.236	0.178	-1.320	0.774
Duration × Object manipulation						
contrast			estimate	SE	z.ratio	*P*
Long,No	-	Short,No	-0.477	0.088	-5.449	**<0.0001**
Long,No	-	Long,Yes	-0.119	0.167	-0.713	0.892
Short,No	-	Short,Yes	0.170	0.091	1.868	0.242
Long,Yes	-	Short,Yes	-0.187	0.121	-1.544	0.411
Sensory modality × Signaller's hierarchical rank						
contrast			estimate	SE	z.ratio	*P*
Auditory,Dominant	-	Tactile,Dominant	0.264	0.278	0.947	0.990
Auditory,Dominant	-	Visual,Dominant	0.218	0.283	0.769	0.998
Auditory,Dominant	-	Auditory,Intermediate	0.968	0.324	2.989	0.069
Auditory,Dominant	-	Auditory,Subordinate	-0.237	0.358	-0.662	0.999
Tactile,Dominant	-	Visual,Dominant	-0.046	0.263	-0.173	1.000
Tactile,Dominant	-	Tactile,Intermediate	0.683	0.252	2.709	0.145
Tactile,Dominant	-	Tactile,Subordinate	0.375	0.272	1.377	0.907
Visual,Dominant	-	Visual,Intermediate	0.361	0.292	1.237	0.949
Visual,Dominant	-	Visual,Subordinate	0.419	0.315	1.329	0.923
Auditory,Intermediate	-	Tactile,Intermediate	-0.022	0.199	-0.111	1.000
Auditory,Intermediate	-	Visual,Intermediate	-0.390	0.199	-1.961	0.571
Auditory,Intermediate	-	Auditory,Subordinate	-1.205	0.145	-8.288	**<0.0001**
Tactile,Intermediate	-	Visual,Intermediate	-0.368	0.198	-1.854	0.646
Tactile,Intermediate	-	Tactile,Subordinate	-0.307	0.126	-2.438	0.263
Visual,Intermediate	-	Visual,Subordinate	0.058	0.117	0.495	1.000
Auditory,Subordinate	-	Tactile,Subordinate	0.876	0.214	4.099	**0.001**
Auditory,Subordinate	-	Visual,Subordinate	0.873	0.214	4.082	**0.002**
Tactile,Subordinate	-	Visual,Subordinate	-0.002	0.207	-0.011	1.000

Table A2. continued

Sensory modality × Affiliation						
contrast			estimate	SE	z.ratio	*P*
Auditory,Strong	-	Tactile,Strong	0.343	0.171	2.008	0.538
Auditory,Strong	-	Visual,Strong	0.234	0.167	1.405	0.896
Auditory,Strong	-	Auditory,Low	-0.085	0.097	-0.882	0.994
Auditory,Strong	-	Auditory,Medium	0.210	0.100	2.106	0.469
Tactile,Strong	-	Visual,Strong	-0.109	0.174	-0.626	1.000
Tactile,Strong	-	Tactile,Low	0.173	0.102	1.703	0.745
Tactile,Strong	-	Tactile,Medium	0.040	0.103	0.387	1.000
Visual,Strong	-	Visual,Low	0.237	0.089	2.678	0.156
Visual,Strong	-	Visual,Medium	-0.114	0.104	-1.093	0.976
Auditory,Low	-	Tactile,Low	0.602	0.169	3.560	**0.011**
Auditory,Low	-	Visual,Low	0.557	0.161	3.466	**0.016**
Auditory,Low	-	Auditory,Medium	0.296	0.107	2.761	0.127
Tactile,Low	-	Visual,Low	-0.045	0.171	-0.261	1.000
Tactile,Low	-	Tactile,Medium	-0.134	0.122	-1.098	0.975
Visual,Low	-	Visual,Medium	-0.351	0.112	-3.134	**0.046**
Auditory,Medium	-	Tactile,Medium	0.172	0.192	0.899	0.993
Auditory,Medium	-	Visual,Medium	-0.090	0.190	-0.472	1.000
Tactile,Medium	-	Visual,Medium	-0.262	0.198	-1.323	0.925
Kinship × Sharing degree						
contrast			estimate	SE	z.ratio	*P*
Parent-infant,Low	-	Siblings,Low	-0.147	0.176	-0.833	0.961
Parent-infant,Low	-	Unrelated,Low	-0.327	0.167	-1.959	0.366
Parent-infant,Low	-	Parent-infant,High	-0.143	0.215	-0.668	0.985
Siblings,Low	-	Unrelated,Low	-0.181	0.167	-1.080	0.890
Siblings,Low	-	Siblings,High	0.015	0.183	0.084	1.000
Unrelated,Low	-	Unrelated,High	0.353	0.186	1.895	0.405
Parent-infant,High	-	Siblings,High	0.012	0.147	0.081	1.000
Parent-infant,High	-	Unrelated,High	0.169	0.117	1.449	0.697
Siblings,High	-	Unrelated,High	0.157	0.132	1.187	0.843
Duration × Signaller's sex						
contrast			estimate	SE	z.ratio	*P*
Long,F	-	Short,F	-0.168	0.103	-1.630	0.361
Long,F	-	Long,M	0.446	0.108	4.113	**0.0002**
Short,F	-	Short,M	0.117	0.074	1.590	0.384
Long,M	-	Short,M	-0.496	0.100	-4.988	**<0.0001**
Recipient's age class × Duration						
contrast			estimate	SE	z.ratio	*P*
Ado.,Long	-	Inf.,Long	-0.282	0.443	-0.637	1.000
Ado.,Long	-	Juv.,Long	0.166	0.293	0.566	1.000
Ado.,Long	-	M.adu.,Long	-0.501	0.429	-1.167	0.977
Ado.,Long	-	Y.adu.,Long	0.514	0.240	2.145	0.496
Ado.,Long	-	Ado.,Short	0.000	0.109	0.004	1.000
Inf.,Long	-	Juv.,Long	0.448	0.470	0.952	0.995
Inf.,Long	-	M.adu.,Long	-0.218	0.573	-0.382	1.000
Inf.,Long	-	Y.adu.,Long	0.796	0.507	1.572	0.862
Inf.,Long	-	Inf.,Short	-0.321	0.109	-2.934	0.096
Juv.,Long	-	M.adu.,Long	-0.667	0.471	-1.415	0.923
Juv.,Long	-	Y.adu.,Long	0.348	0.342	1.017	0.991
Juv.,Long	-	Juv.,Short	-0.455	0.103	-4.431	**0.0004**
M.adu.,Long	-	Y.adu.,Long	1.015	0.477	2.129	0.507
M.adu.,Long	-	M.adu.,Short	-0.474	0.225	-2.104	0.525
Y.adu.,Long	-	Y.adu.,Short	-0.410	0.137	-3.000	0.080
Ado.,Short	-	Inf.,Short	-0.604	0.425	-1.421	0.921
Ado.,Short	-	Juv.,Short	-0.290	0.272	-1.067	0.988
Ado.,Short	-	M.adu.,Short	-0.976	0.376	-2.597	0.219
Ado.,Short	-	Y.adu.,Short	0.104	0.205	0.505	1.000
Inf.,Short	-	Juv.,Short	0.314	0.455	0.689	1.000
Inf.,Short	-	M.adu.,Short	-0.372	0.535	-0.695	1.000
Inf.,Short	-	Y.adu.,Short	0.707	0.486	1.456	0.909
Juv.,Short	-	M.adu.,Short	-0.686	0.422	-1.624	0.837
Juv.,Short	-	Y.adu.,Short	0.394	0.319	1.233	0.967
M.adu.,Short	-	Y.adu.,Short	1.079	0.422	2.556	0.239

Table A2. continued

Signaller's age class × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
Ado.,Auditory	-	Inf.,Auditory	2.128	0.206	10.305	**<0.0001**
Ado.,Auditory	-	Juv.,Auditory	1.633	0.200	8.144	**<0.0001**
Ado.,Auditory	-	M.adu.,Auditory	-0.805	0.741	-1.086	0.999
Ado.,Auditory	-	Y.adu.,Auditory	0.145	0.270	0.539	1.000
Ado.,Auditory	-	Ado.,Tactile	0.838	0.184	4.564	**0.001**
Ado.,Auditory	-	Ado.,Visual	0.867	0.188	4.608	**0.0004**
Inf.,Auditory	-	Juv.,Auditory	-0.495	0.140	-3.545	**0.030**
Inf.,Auditory	-	M.adu.,Auditory	-2.932	0.767	-3.823	**0.011**
Inf.,Auditory	-	Y.adu.,Auditory	-1.982	0.329	-6.021	**<0.0001**
Inf.,Auditory	-	Inf.,Tactile	-0.781	0.223	-3.498	**0.036**
Inf.,Auditory	-	Inf.,Visual	-1.023	0.221	-4.635	**0.0004**
Juv.,Auditory	-	M.adu.,Auditory	-2.437	0.766	-3.180	0.094
Juv.,Auditory	-	Y.adu.,Auditory	-1.487	0.313	-4.755	**0.0002**
Juv.,Auditory	-	Juv.,Tactile	-0.497	0.190	-2.619	0.357
Juv.,Auditory	-	Juv.,Visual	-0.729	0.192	-3.799	**0.012**
M.adu.,Auditory	-	Y.adu.,Auditory	0.950	0.723	1.314	0.993
M.adu.,Auditory	-	M.adu.,Tactile	1.241	0.648	1.915	0.846
M.adu.,Auditory	-	M.adu.,Visual	1.488	0.645	2.306	0.586
Y.adu.,Auditory	-	Y.adu.,Tactile	1.061	0.233	4.555	**0.001**
Y.adu.,Auditory	-	Y.adu.,Visual	0.566	0.243	2.324	0.572
Ado.,Tactile	-	Inf.,Tactile	0.509	0.184	2.771	0.263
Ado.,Tactile	-	Juv.,Tactile	0.298	0.175	1.705	0.932
Ado.,Tactile	-	M.adu.,Tactile	-0.401	0.513	-0.783	1.000
Ado.,Tactile	-	Y.adu.,Tactile	0.369	0.232	1.590	0.961
Ado.,Tactile	-	Ado.,Visual	0.029	0.181	0.161	1.000
Inf.,Tactile	-	Juv.,Tactile	-0.210	0.150	-1.400	0.988
Inf.,Tactile	-	M.adu.,Tactile	-0.910	0.526	-1.731	0.924
Inf.,Tactile	-	Y.adu.,Tactile	-0.140	0.285	-0.492	1.000
Inf.,Tactile	-	Inf.,Visual	-0.241	0.226	-1.066	0.999
Juv.,Tactile	-	M.adu.,Tactile	-0.699	0.525	-1.333	0.992
Juv.,Tactile	-	Y.adu.,Tactile	0.070	0.268	0.263	1.000
Juv.,Tactile	-	Juv.,Visual	-0.232	0.191	-1.214	0.997
M.adu.,Tactile	-	Y.adu.,Tactile	0.770	0.520	1.480	0.979
M.adu.,Tactile	-	M.adu.,Visual	0.247	0.591	0.418	1.000
Y.adu.,Tactile	-	Y.adu.,Visual	-0.495	0.252	-1.966	0.819
Ado.,Visual	-	Inf.,Visual	0.238	0.168	1.418	0.986
Ado.,Visual	-	Juv.,Visual	0.037	0.168	0.220	1.000
Ado.,Visual	-	M.adu.,Visual	-0.183	0.624	-0.294	1.000
Ado.,Visual	-	Y.adu.,Visual	-0.156	0.246	-0.635	1.000
Inf.,Visual	-	Juv.,Visual	-0.201	0.138	-1.457	0.982
Inf.,Visual	-	M.adu.,Visual	-0.421	0.651	-0.647	1.000
Inf.,Visual	-	Y.adu.,Visual	-0.394	0.303	-1.303	0.994
Juv.,Visual	-	M.adu.,Visual	-0.220	0.646	-0.341	1.000
Juv.,Visual	-	Y.adu.,Visual	-0.193	0.290	-0.666	1.000
M.adu.,Visual	-	Y.adu.,Visual	0.027	0.604	0.045	1.000
Signaller's sex × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
F,Auditory	-	M,Auditory	0.370	0.107	3.470	**0.007**
F,Auditory	-	F,Tactile	0.596	0.177	3.365	**0.010**
F,Auditory	-	F,Visual	0.144	0.170	0.844	0.959
M,Auditory	-	M,Tactile	0.149	0.165	0.902	0.946
M,Auditory	-	M,Visual	0.324	0.158	2.054	0.312
F,Tactile	-	M,Tactile	-0.077	0.095	-0.808	0.966
F,Tactile	-	F,Visual	-0.452	0.181	-2.504	0.123
M,Tactile	-	M,Visual	0.175	0.169	1.037	0.906
F,Visual	-	M,Visual	0.551	0.100	5.534	**<0.0001**

Table A2. continued

Zoo × Sensory modality						
contrast			estimate	SE	z.ratio	*P*
Apenheul,Auditory	-	Burgers,Auditory	0.565	0.275	2.055	0.505
Apenheul,Auditory	-	Vallee,Auditory	1.813	0.311	5.828	**<0.0001**
Apenheul,Auditory	-	Apenheul,Tactile	1.268	0.187	6.793	**<0.0001**
Apenheul,Auditory	-	Apenheul,Visual	1.186	0.184	6.431	**<0.0001**
Burgers,Auditory	-	Vallee,Auditory	1.248	0.368	3.391	**0.020**
Burgers,Auditory	-	Burgers,Tactile	-0.062	0.183	-0.338	1.000
Burgers,Auditory	-	Burgers,Visual	-0.013	0.180	-0.072	1.000
Vallee,Auditory	-	Vallee,Tactile	-0.088	0.182	-0.485	1.000
Vallee,Auditory	-	Vallee,Visual	-0.472	0.180	-2.615	0.180
Apenheul,Tactile	-	Burgers,Tactile	-0.765	0.272	-2.814	0.111
Apenheul,Tactile	-	Vallee,Tactile	0.457	0.306	1.494	0.859
Apenheul,Tactile	-	Apenheul,Visual	-0.081	0.186	-0.436	1.000
Burgers,Tactile	-	Vallee,Tactile	1.221	0.373	3.278	**0.029**
Burgers,Tactile	-	Burgers,Visual	0.049	0.189	0.259	1.000
Vallee,Tactile	-	Vallee,Visual	-0.383	0.189	-2.024	0.527
Apenheul,Visual	-	Burgers,Visual	-0.634	0.258	-2.457	0.254
Apenheul,Visual	-	Vallee,Visual	0.155	0.307	0.503	1.000
Burgers,Visual	-	Vallee,Visual	0.789	0.363	2.173	0.424
Recipient's sex × Object manipulation						
contrast			estimate	SE	z.ratio	*P*
F,No	-	M,No	-0.513	0.244	-2.105	0.151
F,No	-	F,Yes	-0.081	0.121	-0.672	0.908
M,No	-	M,Yes	0.132	0.126	1.054	0.718
F,Yes	-	M,Yes	-0.299	0.252	-1.188	0.635
Sharing degree × Signaller's age class						
contrast			estimate	SE	z.ratio	*P*
Low,Ado.	-	High,Ado.	0.023	0.151	0.155	1.000
Low,Ado.	-	Low,Inf.	1.137	0.166	6.853	**<0.0001**
Low,Ado.	-	Low,Juv.	0.653	0.175	3.736	**0.007**
Low,Ado.	-	Low,M.adu.	-0.809	0.691	-1.171	0.977
Low,Ado.	-	Low,Y.adu.	0.161	0.250	0.643	1.000
High,Ado.	-	High,Inf.	0.780	0.129	6.033	**<0.0001**
High,Ado.	-	High,Juv.	0.659	0.143	4.593	**0.0002**
High,Ado.	-	High,M.adu.	-0.117	0.490	-0.238	1.000
High,Ado.	-	High,Y.adu.	0.078	0.167	0.466	1.000
Low,Inf.	-	High,Inf.	-0.334	0.157	-2.120	0.513
Low,Inf.	-	Low,Juv.	-0.483	0.151	-3.201	**0.045**
Low,Inf.	-	Low,M.adu.	-1.946	0.696	-2.798	0.137
Low,Inf.	-	Low,Y.adu.	-0.976	0.283	-3.446	**0.020**
High,Inf.	-	High,Juv.	-0.121	0.111	-1.090	0.986
High,Inf.	-	High,M.adu.	-0.896	0.505	-1.777	0.750
High,Inf.	-	High,Y.adu.	-0.702	0.209	-3.356	**0.027**
Low,Juv.	-	High,Juv.	0.029	0.153	0.191	1.000
Low,Juv.	-	Low,M.adu.	-1.463	0.700	-2.088	0.536
Low,Juv.	-	Low,Y.adu.	-0.492	0.272	-1.811	0.729
High,Juv.	-	High,M.adu.	-0.776	0.507	-1.531	0.880
High,Juv.	-	High,Y.adu.	-0.581	0.211	-2.749	0.155
Low,M.adu.	-	High,M.adu.	0.716	0.640	1.119	0.983
Low,M.adu.	-	Low,Y.adu.	0.970	0.700	1.386	0.932
High,M.adu.	-	High,Y.adu.	0.194	0.493	0.394	1.000
Low,Y.adu.	-	High,Y.adu.	-0.060	0.224	-0.267	1.000
Sharing degree × Signaller's sex						
contrast			estimate	SE	z.ratio	*P*
Low,F	-	High,F	-0.124	0.180	-0.688	0.902
Low,F	-	Low,M	0.083	0.098	0.843	0.834
High,F	-	High,M	0.481	0.073	6.627	**<0.0001**
Low,M	-	High,M	0.274	0.179	1.529	0.420

Table A2. continued

Sharing degree × Zoo						
contrast			estimate	SE	z.ratio	*P*
Low,Apenheul	-	High,Apenheul	0.347	0.195	1.783	0.477
Low,Apenheul	-	Low,Burgers	-0.161	0.277	-0.584	0.992
Low,Apenheul	-	Low,Vallee	1.100	0.312	3.522	**0.006**
High,Apenheul	-	High,Burgers	-0.395	0.247	-1.596	0.601
High,Apenheul	-	High,Vallee	0.516	0.292	1.770	0.485
Low,Burgers	-	High,Burgers	0.114	0.181	0.631	0.989
Low,Burgers	-	Low,Vallee	1.261	0.370	3.408	**0.009**
High,Burgers	-	High,Vallee	0.911	0.355	2.565	0.106
Low,Vallee	-	High,Vallee	-0.236	0.202	-1.170	0.851
Zoo × Signaller's hierarchical rank						
contrast			estimate	SE	z.ratio	*P*
Apenheul,Dominant	-	Burgers,Dominant	-0.695	0.319	-2.179	0.420
Apenheul,Dominant	-	Vallee,Dominant	-0.338	0.566	-0.597	1.000
Apenheul,Dominant	-	Apenheul,Intermediate	-0.249	0.265	-0.940	0.991
Apenheul,Dominant	-	Apenheul,Subordinate	-0.457	0.255	-1.794	0.687
Burgers,Dominant	-	Vallee,Dominant	0.356	0.614	0.581	1.000
Burgers,Dominant	-	Burgers,Intermediate	0.296	0.177	1.674	0.763
Burgers,Dominant	-	Burgers,Subordinate	0.247	0.222	1.117	0.972
Vallee,Dominant	-	Vallee,Intermediate	1.965	0.559	3.516	**0.013**
Vallee,Dominant	-	Vallee,Subordinate	0.767	0.559	1.373	0.908
Apenheul,Intermediate	-	Burgers,Intermediate	-0.149	0.296	-0.505	1.000
Apenheul,Intermediate	-	Vallee,Intermediate	1.876	0.303	6.198	**<0.0001**
Apenheul,Intermediate	-	Apenheul,Subordinate	-0.208	0.113	-1.848	0.650
Burgers,Intermediate	-	Vallee,Intermediate	2.025	0.351	5.766	**<0.0001**
Burgers,Intermediate	-	Burgers,Subordinate	-0.049	0.165	-0.294	1.000
Vallee,Intermediate	-	Vallee,Subordinate	-1.197	0.111	-10.776	**<0.0001**
Apenheul,Subordinate	-	Burgers,Subordinate	0.010	0.270	0.038	1.000
Apenheul,Subordinate	-	Vallee,Subordinate	0.887	0.282	3.144	**0.044**
Burgers,Subordinate	-	Vallee,Subordinate	0.876	0.337	2.604	0.185

Table A2. continued

Recipient's age class × Signaller's age class						
contrast			estimate	SE	z.ratio	*P*
Ado.,Ado.	-	Inf.,Ado.	-0.680	0.510	-1.334	1.000
Ado.,Ado.	-	Juv.,Ado.	-0.200	0.340	-0.588	1.000
Ado.,Ado.	-	M.adu.,Ado.	-1.036	0.383	-2.707	0.531
Ado.,Ado.	-	Y.adu.,Ado.	-0.020	0.236	-0.086	1.000
Ado.,Ado.	-	Ado.,Inf.	0.711	0.163	4.356	**0.003**
Ado.,Ado.	-	Ado.,Juv.	0.612	0.173	3.540	0.073
Ado.,Ado.	-	Ado.,M.adu.	-1.042	0.742	-1.405	1.000
Ado.,Ado.	-	Ado.,Y.adu.	-0.011	0.283	-0.038	1.000
Inf.,Ado.	-	Juv.,Ado.	0.480	0.515	0.932	1.000
Inf.,Ado.	-	M.adu.,Ado.	-0.357	0.539	-0.662	1.000
Inf.,Ado.	-	Y.adu.,Ado.	0.660	0.536	1.231	1.000
Inf.,Ado.	-	Inf.,Inf.	0.783	0.176	4.445	**0.002**
Inf.,Ado.	-	Inf.,Juv.	0.561	0.192	2.927	0.360
Inf.,Ado.	-	Inf.,M.adu.	0.675	0.648	1.042	1.000
Inf.,Ado.	-	Inf.,Y.adu.	-0.566	0.438	-1.291	1.000
Juv.,Ado.	-	M.adu.,Ado.	-0.836	0.442	-1.894	0.975
Juv.,Ado.	-	Y.adu.,Ado.	0.180	0.353	0.510	1.000
Juv.,Ado.	-	Juv.,Inf.	1.126	0.154	7.303	**<0.0001**
Juv.,Ado.	-	Juv.,Juv.	0.692	0.166	4.174	**0.007**
Juv.,Ado.	-	Juv.,M.adu.	-1.091	0.627	-1.739	0.992
Juv.,Ado.	-	Juv.,Y.adu.	0.230	0.245	0.939	1.000
M.adu.,Ado.	-	Y.adu.,Ado.	1.016	0.377	2.694	0.541
M.adu.,Ado.	-	M.adu.,Inf.	0.882	0.241	3.666	**0.049**
M.adu.,Ado.	-	M.adu.,Juv.	0.904	0.276	3.279	0.158
M.adu.,Ado.	-	M.adu.,M.adu.	-0.288	1.434	-0.201	1.000
M.adu.,Ado.	-	M.adu.,Y.adu.	0.262	0.348	0.755	1.000
Y.adu.,Ado.	-	Y.adu.,Inf.	1.289	0.244	5.288	**<0.0001**
Y.adu.,Ado.	-	Y.adu.,Juv.	0.512	0.216	2.369	0.789
Y.adu.,Ado.	-	Y.adu.,M.adu.	-0.568	0.463	-1.227	1.000
Y.adu.,Ado.	-	Y.adu.,Y.adu.	0.680	0.206	3.299	0.149
Ado.,Inf.	-	Inf.,Inf.	-0.608	0.508	-1.195	1.000
Ado.,Inf.	-	Juv.,Inf.	0.216	0.345	0.626	1.000
Ado.,Inf.	-	M.adu.,Inf.	-0.865	0.361	-2.394	0.772
Ado.,Inf.	-	Y.adu.,Inf.	0.559	0.237	2.361	0.794
Ado.,Inf.	-	Ado.,Juv.	-0.099	0.155	-0.637	1.000
Ado.,Inf.	-	Ado.,M.adu.	-1.753	0.742	-2.363	0.793
Ado.,Inf.	-	Ado.,Y.adu.	-0.721	0.277	-2.603	0.615
Inf.,Inf.	-	Juv.,Inf.	0.824	0.502	1.642	0.996
Inf.,Inf.	-	M.adu.,Inf.	-0.258	0.534	-0.482	1.000
Inf.,Inf.	-	Y.adu.,Inf.	1.166	0.539	2.162	0.901
Inf.,Inf.	-	Inf.,Juv.	-0.222	0.132	-1.680	0.995
Inf.,Inf.	-	Inf.,M.adu.	-0.108	0.651	-0.166	1.000
Inf.,Inf.	-	Inf.,Y.adu.	-1.348	0.450	-2.998	0.311
Juv.,Inf.	-	M.adu.,Inf.	-1.081	0.433	-2.498	0.697
Juv.,Inf.	-	Y.adu.,Inf.	0.343	0.374	0.916	1.000
Juv.,Inf.	-	Juv.,Juv.	-0.434	0.123	-3.515	0.079
Juv.,Inf.	-	Juv.,M.adu.	-2.217	0.634	-3.498	0.084
Juv.,Inf.	-	Juv.,Y.adu.	-0.896	0.284	-3.161	0.213
M.adu.,Inf.	-	Y.adu.,Inf.	1.424	0.385	3.702	**0.043**
M.adu.,Inf.	-	M.adu.,Juv.	0.022	0.229	0.097	1.000
M.adu.,Inf.	-	M.adu.,M.adu.	-1.170	1.448	-0.808	1.000
M.adu.,Inf.	-	M.adu.,Y.adu.	-0.619	0.350	-1.771	0.989
Y.adu.,Inf.	-	Y.adu.,Juv.	-0.778	0.218	-3.569	0.067
Y.adu.,Inf.	-	Y.adu.,M.adu.	-1.858	0.497	-3.737	**0.038**
Y.adu.,Inf.	-	Y.adu.,Y.adu.	-0.609	0.273	-2.230	0.870
Ado.,Juv.	-	Inf.,Juv.	-0.731	0.503	-1.453	0.999
Ado.,Juv.	-	Juv.,Juv.	-0.119	0.334	-0.357	1.000
Ado.,Juv.	-	M.adu.,Juv.	-0.744	0.394	-1.887	0.976
Ado.,Juv.	-	Y.adu.,Juv.	-0.120	0.227	-0.528	1.000
Ado.,Juv.	-	Ado.,M.adu.	-1.654	0.751	-2.201	0.884
Ado.,Juv.	-	Ado.,Y.adu.	-0.622	0.296	-2.104	0.924

Inf.,Juv.	-	Juv.,Juv.	0.611	0.504	1.214	1.000
Inf.,Juv.	-	M.adu.,Juv.	-0.014	0.551	-0.025	1.000
Inf.,Juv.	-	Y.adu.,Juv.	0.611	0.533	1.145	1.000
Inf.,Juv.	-	Inf.,M.adu.	0.114	0.653	0.175	1.000
Inf.,Juv.	-	Inf.,Y.adu.	-1.126	0.452	-2.491	0.703
Juv.,Juv.	-	M.adu.,Juv.	-0.625	0.452	-1.382	1.000
Juv.,Juv.	-	Y.adu.,Juv.	-0.001	0.358	-0.003	1.000
Juv.,Juv.	-	Juv.,M.adu.	-1.783	0.637	-2.800	0.456
Juv.,Juv.	-	Juv.,Y.adu.	-0.462	0.285	-1.623	0.997
M.adu.,Juv.	-	Y.adu.,Juv.	0.624	0.394	1.583	0.998
M.adu.,Juv.	-	M.adu.,M.adu.	-1.192	1.454	-0.820	1.000
M.adu.,Juv.	-	M.adu.,Y.adu.	-0.641	0.369	-1.740	0.992
Y.adu.,Juv.	-	Y.adu.,M.adu.	-1.080	0.487	-2.219	0.875
Y.adu.,Juv.	-	Y.adu.,Y.adu.	0.169	0.257	0.656	1.000
Ado.,M.adu.	-	Inf.,M.adu.	1.037	0.596	1.740	0.992
Ado.,M.adu.	-	Juv.,M.adu.	-0.248	0.704	-0.353	1.000
Ado.,M.adu.	-	M.adu.,M.adu.	-0.282	1.412	-0.200	1.000
Ado.,M.adu.	-	Y.adu.,M.adu.	0.454	0.783	0.580	1.000
Ado.,M.adu.	-	Ado.,Y.adu.	1.032	0.742	1.390	1.000
Inf.,M.adu.	-	Juv.,M.adu.	-1.286	0.680	-1.892	0.976
Inf.,M.adu.	-	M.adu.,M.adu.	-1.320	1.362	-0.969	1.000
Inf.,M.adu.	-	Y.adu.,M.adu.	-0.584	0.773	-0.755	1.000
Inf.,M.adu.	-	Inf.,Y.adu.	-1.240	0.719	-1.726	0.992
Juv.,M.adu.	-	M.adu.,M.adu.	-0.034	1.423	-0.024	1.000
Juv.,M.adu.	-	Y.adu.,M.adu.	0.702	0.703	0.999	1.000
Juv.,M.adu.	-	Juv.,Y.adu.	1.321	0.629	2.100	0.925
M.adu.,M.adu.	-	Y.adu.,M.adu.	0.736	1.503	0.490	1.000
M.adu.,M.adu.	-	M.adu.,Y.adu.	0.551	1.458	0.378	1.000
Y.adu.,M.adu.	-	Y.adu.,Y.adu.	1.249	0.457	2.731	0.512
Ado.,Y.adu.	-	Inf.,Y.adu.	-1.235	0.629	-1.962	0.963
Ado.,Y.adu.	-	Juv.,Y.adu.	0.041	0.370	0.110	1.000
Ado.,Y.adu.	-	M.adu.,Y.adu.	-0.763	0.423	-1.803	0.987
Ado.,Y.adu.	-	Y.adu.,Y.adu.	0.671	0.225	2.979	0.324
Inf.,Y.adu.	-	Juv.,Y.adu.	1.276	0.636	2.006	0.953
Inf.,Y.adu.	-	M.adu.,Y.adu.	0.471	0.676	0.698	1.000
Inf.,Y.adu.	-	Y.adu.,Y.adu.	1.906	0.630	3.023	0.294
Juv.,Y.adu.	-	M.adu.,Y.adu.	-0.804	0.452	-1.780	0.989
Juv.,Y.adu.	-	Y.adu.,Y.adu.	0.630	0.367	1.719	0.993
M.adu.,Y.adu.	-	Y.adu.,Y.adu.	1.434	0.426	3.367	0.124
Signaller's age class × Recipient's sex						
contrast			estimate	SE	z.ratio	*P*
Ado.,F	-	Inf.,F	0.903	0.141	6.409	**<0.0001**
Ado.,F	-	Juv.,F	0.550	0.161	3.427	**0.022**
Ado.,F	-	M.adu.,F	-1.061	0.521	-2.035	0.574
Ado.,F	-	Y.adu.,F	0.026	0.203	0.130	1.000
Ado.,F	-	Ado.,M	-0.747	0.270	-2.770	0.147
Inf.,F	-	Juv.,F	-0.352	0.125	-2.823	0.129
Inf.,F	-	M.adu.,F	-1.964	0.530	-3.706	**0.008**
Inf.,F	-	Y.adu.,F	-0.876	0.228	-3.840	**0.005**
Inf.,F	-	Inf.,M	-0.636	0.265	-2.399	0.326
Juv.,F	-	M.adu.,F	-1.612	0.537	-3.002	0.080
Juv.,F	-	Y.adu.,F	-0.524	0.235	-2.226	0.439
Juv.,F	-	Juv.,M	-0.536	0.266	-2.015	0.588
M.adu.,F	-	Y.adu.,F	1.088	0.527	2.063	0.554
M.adu.,F	-	M.adu.,M	0.449	0.426	1.054	0.989
Y.adu.,F	-	Y.adu.,M	-0.561	0.291	-1.930	0.648
Ado.,M	-	Inf.,M	1.014	0.142	7.150	**<0.0001**
Ado.,M	-	Juv.,M	0.762	0.155	4.923	**<0.0001**
Ado.,M	-	M.adu.,M	0.135	0.574	0.235	1.000
Ado.,M	-	Y.adu.,M	0.212	0.209	1.014	0.992
Inf.,M	-	Juv.,M	-0.252	0.125	-2.010	0.592
Inf.,M	-	M.adu.,M	-0.879	0.582	-1.509	0.889
Inf.,M	-	Y.adu.,M	-0.801	0.244	-3.290	**0.034**
Juv.,M	-	M.adu.,M	-0.627	0.585	-1.072	0.987
Juv.,M	-	Y.adu.,M	-0.549	0.244	-2.256	0.418
M.adu.,M	-	Y.adu.,M	0.077	0.581	0.133	1.000

Table A2. continued

Signaller's sex × Zoo						
contrast			estimate	SE	z.ratio	*P*
F,Apenheul	-	M,Apenheul	0.238	0.091	2.612	0.095
F,Apenheul	-	F,Burgers	-0.166	0.258	-0.642	0.988
F,Apenheul	-	F,Vallee	0.630	0.307	2.048	0.315
M,Apenheul	-	M,Burgers	-0.390	0.258	-1.515	0.655
M,Apenheul	-	M,Vallee	0.986	0.304	3.248	**0.015**
F,Burgers	-	M,Burgers	0.013	0.099	0.129	1.000
F,Burgers	-	F,Vallee	0.795	0.367	2.165	0.254
M,Burgers	-	M,Vallee	1.377	0.360	3.829	**0.002**
F,Vallee	-	M,Vallee	0.594	0.137	4.324	**0.0002**

Figure captions

Figure 1: Positions of recipient in relation to signaller during an interaction. Heads of subjects represented by arrows (oriented ahead of subjects). Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field. Recipient's Visual Fields: signaller in recipient's left (RVF_L) or right (RVF_R) visual field. Dotted lines: recipient, unbroken lines: signaller, bold lines: left hemiface, thin lines: right hemiface. The different possible positions are ordered by increasing occurrence frequency.

Figure 2: Adjusted probability (± SE) of right-hand use for each sensory modality. (a) Interaction with Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field. (b) Interaction with Recipient's Visual Fields: signaller in the recipient's left (RVF_L) or right (RVF_R) visual field. Vertically striped bars: tactile gestures. Squared bars: auditory gestures. Diagonally striped bars: visual gestures. Tukey test: $^{**}P < 0.01$, $^{***}P < 0.001$.

Figure 3: Adjusted probability (± SE) of right-hand use for each emotional context. Interaction with Interaction with Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field. Black bars: negative emotional context. Open bars: positive emotional context. Tukey test: $^{*}P < 0.05$, $^{***}P < 0.001$.

Figure 4: Adjusted probability (± SE) of right-hand use for gestures with and without an object in relation to the position of signaller in recipient's visual field and conversely. (a) Interaction with Signaller's Visual Fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field. (b) Interaction with Recipient's Visual Fields: signaller in recipient's left (RVF_L) or right (RVF_R) visual field. Grey bars: Gestures with an object. Diagonally striped bars: Gestures without an object. Tukey test: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Figure 5: Adjusted probability (± SE) of right-hand use for each sensory modality. Interaction with signaller's hierarchical rank. Vertically striped bars: tactile gestures. Checkered bars: auditory gestures. Diagonally striped bars: visual gestures Tukey test: $^{**}P < 0.01$, $^{***}P < 0.001$.

Figure 6: Adjusted probability (± SE) of right-hand use for each signaller's age class. Interaction with recipient's age class. Gradual range of grey bars: signaller's age classes from light grey (Infant) to dark grey (Mature adult). Tukey test: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Figure 7: Adjusted probability (± SE) of right-hand use for each sensory modality. Interaction with signaller's sex. Vertically striped bars: tactile gestures. Checkered bars: auditory gestures. Diagonally striped bars: visual gestures Tukey test: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Figure 1

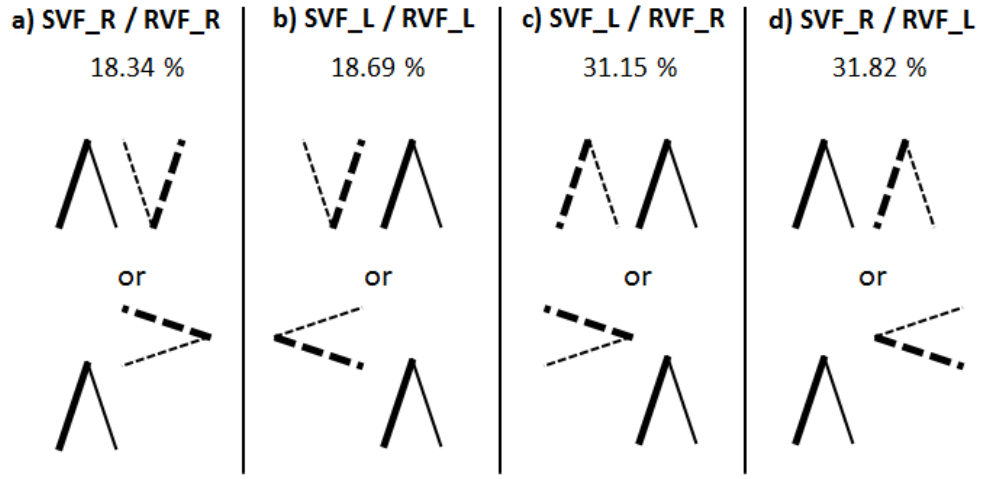


Figure 2

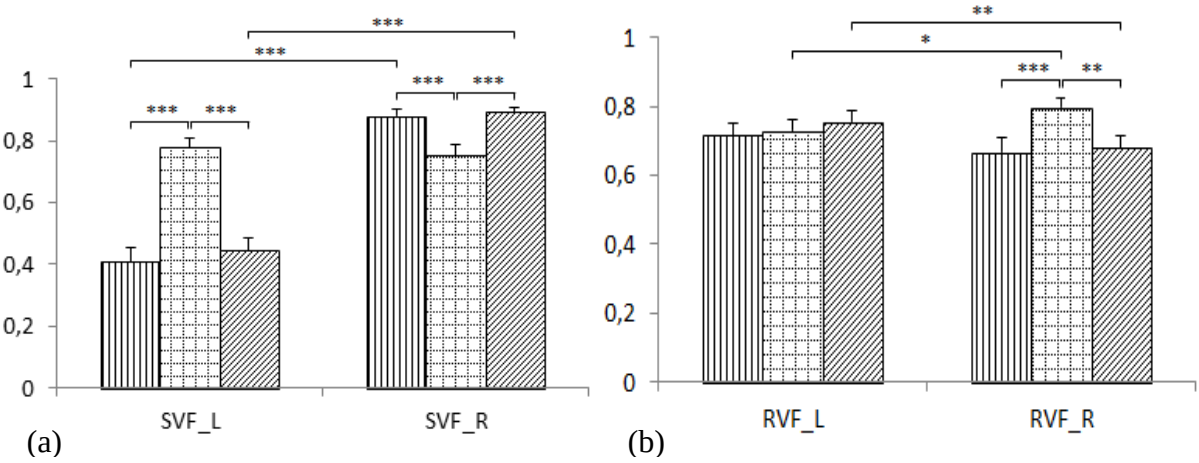


Figure 3

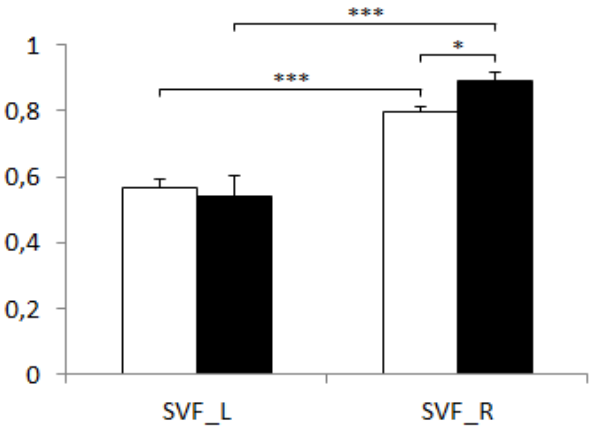


Figure 4

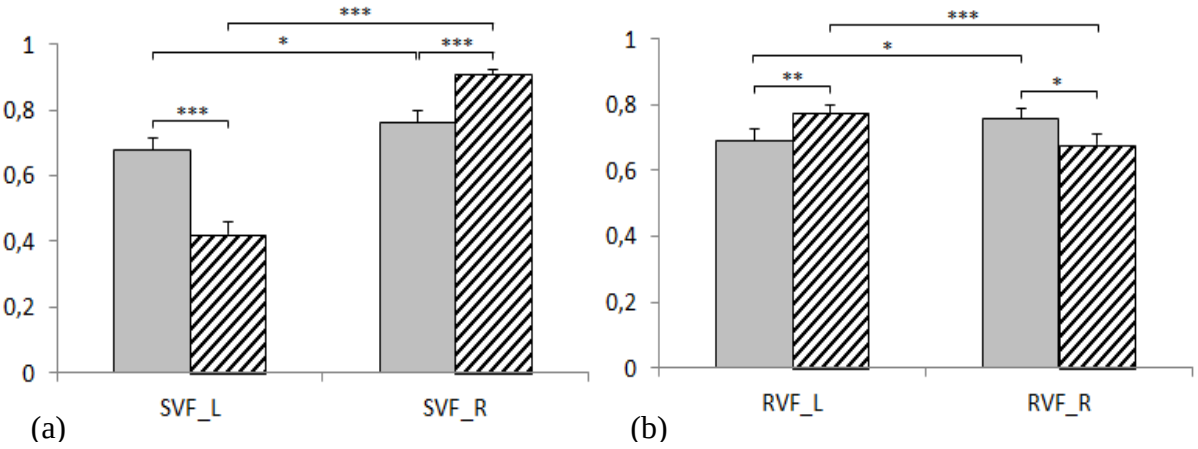


Figure 5

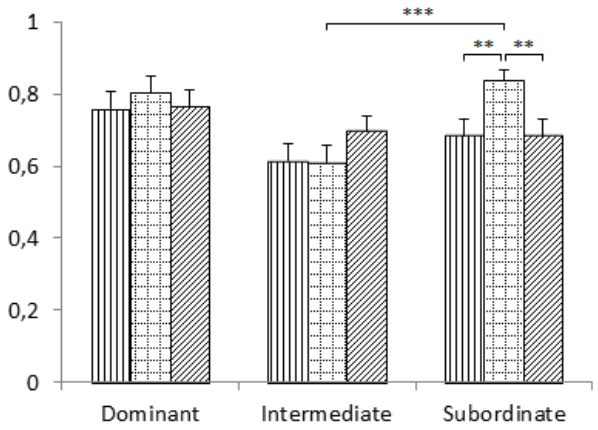


Figure 6

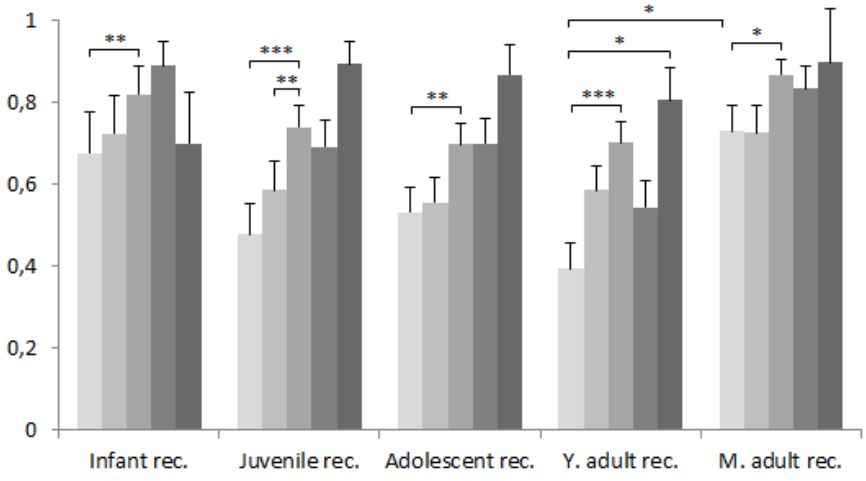
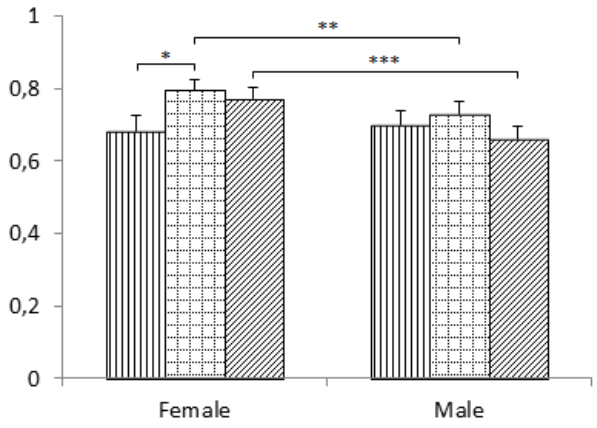


Figure 7



CHAPTER 4

Captive chimpanzees' manual laterality in the context of tool use

Article 3

Manuscript to be submitted in Animal Cognition

Captive chimpanzees' manual laterality in the context of tool use: influence of communication and sociodemographic factors

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Summary of Article 3

Questions: Some studies have already compared manual asymmetry between manipulation and gestural communication, but as far as we know, no comparisons have 1) taken simultaneously into account the potential influence of multiple factors and their interactions (mandatory requirement to assess effects particular to the function), 2) investigated the effects of sociodemographic factors on laterality considering several narrow categories of age (e.g. immature, adolescent, young and mature adult and elder) and hierarchical rank (e.g. dominant, intermediate and subordinate), or 3) considered only purely intraspecific communication (only relevant in an evolutionary perspective) as well as activities involving using a tool (hypothesized to have facilitated the emergence of humans' language capacities,). The present study is the first to address these issues. We questioned first, whether hand laterality differed at the population level for each tool-use activity considered; second, whether sociodemographic factors influenced manual laterality for tool use in intraspecific gestures and non-communication actions.

Methods: Data were collected through observation of three groups of captive chimpanzees including 39 subjects in all. We assessed their hand laterality in real-life social-ecological situations considering non-communication actions similar to termite fishing and five frequent conspecific-directed gestures involving a communication tool. We considered the following potentially influential sociodemographic characteristics: age, sex, group/zoo, and hierarchy.

Results: Our findings evidenced a right-hand bias at the population level for each of the five conspecific-directed gestures involving a tool whereas we did not detect a bias for non-communication tool-use actions. Our findings evidenced that chimpanzees' manual laterality in tool-use was not influenced only by type of activity (communication or manipulation) but was also modulated by individual characteristics, mainly hierarchy, age and, to a lesser extent, sex. More precisely, right-hand use was greater for gestures than for manipulation for dominant and immature initiators. On the contrary, subordinates, adolescents, young and mature adults as well as males were more right-handed for manipulation than for gestures. No differences between the two activities were evidenced for intermediates, elders, females as well as for the three groups/zoos.

Conclusion: Our results concerning dominants free from psychological stress in food access contexts, suggest that effects particular to communication on laterality induce a greater right-hand use for gestures than for manipulation. Our findings agree with previous reports indicating that some primate species may have a specific left-hemisphere processing of gestural communication distinct from that of non-communication manual actions.

Captive chimpanzees' manual laterality in the context of tool use: influence of communication and of sociodemographic factors

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Abstract

Understanding variations of apes' laterality between activities is a central issue when investigating the origin and evolution of human hemispheric specialization of manual functions and language. To our knowledge no study has yet compared non-human primates' manual laterality of tool-use in non-communication actions and gestures to assess the effects of communication on laterality. We assessed chimpanzees' laterality in real-life social-ecological situations concerning a non-communication action similar to termite fishing and five frequent conspecific-directed gestures involving a tool. We evaluated, first, manual laterality at the population level for each tool-use activity; second, the influence of sociodemographic factors on manual laterality in both non-communication actions and gestures. Our subjects were 39 captive chimpanzees belonging to three groups. We took into account the following sociodemographic characteristics: age, sex, group, and hierarchy. Significant right-hand biases at the population level were found for each gesture, but not for non-communication tool-use. 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 discussion leads us to 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.

Keywords: object manipulations, gestures, intraspecific communication, *Pan troglodytes*, hemispheric lateralization.

In 1865, Broca made the pioneering discovery that the human brain is asymetrically structured in relation to language functions (Broca 1865). Since Broca's discovery, a vast body of research reported human cerebral lateralization for motor, sensory, cognitive and emotional functions (e.g. Hugdahl & Davidson 2002). Lateralization of brain functions has been put forward to improve cognitive abilities by avoiding replication of functions and hemispheric competition (e.g. Corballis 1989; Bisazza et al. 1998) and by allowing simultaneous processing of different sources of information (e.g. Rogers 2002; Rogers et al. 2004). Among brain functions, handedness is one of the most investigated traits. Concerning manipulation[19] activities, modern humans exhibit a strong preference for right-hand use at the population level (e.g. Hécaen & de Ajuriaguerra 1964; McManus 1991). For instance, 90% of individuals preferentially use their right hand for complex tasks such as writing, bimanual coordinated actions and tool use (e.g. Annett 1985; Fagard 2004; Faurie 2004; Faurie & Raymond 2004). Humans' right-hand preference has also been put in evidence for distinct communication activities. Reports concern speech accompanying gestures (e.g. Dalby et al. 1980, Kimura 1973a, 1973b; Saucier & Elias, 2001) and signs used by adult non-hearing speakers (e.g. Bellugi 1991; Corina et al. 1992 Grossi et al. 1996; Vaid et al. 1989) as well as gestures[20] produced from early infancy on such as POINTING[21] and/or symbolic gestures (e.g. Bates et al. 1986; Blake 2000; Cochet & Vauclair 2010a, 2010b; Vauclair & Imbault 2009; Young et al. 1985). In addition, humans' gestural communication in humans involves brain regions similar to those processing spoken language (i.e. Broca and Wernicke's areas) (e.g. Horwitz et al. 2003; Xu et al. 2009). Interestingly, about 95% of right-handed and between 70 and 85 % of left-handed individuals for manipulation showed a predominance of the left hemisphere of the brain for language (Knecht et al. 2000; Perlaki et al. 2013; for similar findings see Pujol et al. 1999; Tzourio et al. 1998). In sum, these data provided evidence that (a) the left cerebral hemisphere in humans is predominantly involved in manipulation and communication activities, and (b) an ambiguous relationship exists between the direction of handedness for manipulation and lateralization of language. These findings have thus raised the following question: are manual actions performed in the contexts in which manipulations and gestural communication occur controlled by different lateralized cerebral structures?

To address this issue, authors compared hand preference in non-communication and communication scenarios. The majority of studies has been focusing on hand preferences of

[19] From here, we refer to manipulation as manual actions deprived of communication function.
[20] From here, following the Pika's definition of gesture (Pika 2008a, 2008b), the term gesture is restricted to communication functions.
[21] From here, gestures are written in lower capitals.

young children and found that they preferentially use their right hand during purely communicative interactions than when engaging in non-communication actions (Bates et al. 1986; Bonvillian et al. 1997; Vauclair & Imbault 2009; Cochet et al. 2011; Esseily et al. 2011; Meunier et al. 2012). In addition, Cochet and colleagues (2012) provided evidence that adult humans show a greater right-hand use in bimanual manipulative actions than when they POINT without using speech. In addition, there is no difference in the direction of laterality between bimanual manipulative actions and POINTING produced with speech. Currently, the results of these comparative approaches between communication and non-communication activities of humans remain unclear and further investigations are needed.

Another useful approach to the puzzle of brain laterality in relation to language related functions is the comparative approach, which pinpoints similarities and differences to then draw informed inferences about the abilities of our extinct ancestors. The majority of studies has been focusing on non-human primates (hereafter primates), which are not only close phylogenetically (e.g. Silverstein 1997; Seuanez 2012) to humans but show relatively high degrees of similarity concerning the morphology of their hands (e.g. Aiello & Dean 1990; Napier 1962) and the ability to manipulate (e.g. Byrne et al. 2001; Napier 1960). Studies both in captivity and the wild have also reported that some primate species are able to make and to use tools: e.g. bonobos (e.g. Kano 1982), chimpanzees (e.g. McGrew 1992), gorillas (e.g. Grueter et al. 2013), orang-utans (Van Schaik et al. 2003), and capuchins (Perry et al. 2003). Primates are also relevant models to help us explore the evolutionary roots of human language. Indeed, the finding that some primate species, particularly great apes, show laterality while performing gestures has been seen as crucial evidence in favor of the gesture first hypothesis (Corballis 2002, 2003; see also reviews Hopkins et al. 2012; Meguerditchian et al. 2013). This hypothesis is also supported by neuroanatomical studies showing the left cerebral hemisphere predominance in the homologs of the human Broca's and Wernicke's areas in great apes (e.g. Cantalupo & Hopkins 2001; Gannon et al. 1998; Hopkins et al. 2007). Among research investigating laterality of primates' gestural communication, many studies have considered human-directed gestures (i.e. in artificial conditions) of several species including chimpanzees (e.g. Hopkins & Leavens 1998; Hopkins & Cantero 2003; Meguerditchian et al. 2012), olive baboons (e.g. Meguerditchian & Vauclair 2006; Meunier et al. 2012b; Bourjade 2013), Tonkean macaques and tufted capuchins (Meunier et al. 2013) as well as red-capped mangabeys and Campbell's monkeys (Maille et al. 2013). By contrast, there are only few reports about laterality in purely intra-specific communication

(chimpanzees: Fletcher & Weghorst 2005; Meguerditchian et al. 2010a; Hobaiter & Byrne 2013; bonobos: Chapelain 2010; olive baboons: Meguerditchian & Vauclair 2006) although studying communication between conspecifics in real-life social contexts (i.e. close to contexts in which natural selection acts) would be necessary to better understand gestural laterality from an evolutionary point of view.

To investigate whether primates' manual actions performed in manipulations and gestures are controlled by different lateralized cerebral structures, several studies compared manual laterality in both functions (e.g. chimpanzees: Meguerditchian et al. 2010a; red-capped mangabeys and Campbell's monkeys: Maille et al. 2013). These studies found a greater right-hand use in gestures than in non-communication actions thereby supporting the hypothesis that manipulation and communication components would not share the same lateralized cerebral system of some primate species (e.g. Meguerditchian & Vauclair 2009). However, there are some limitations. First, none of these studies has considered purely intraspecific communication in their comparisons. Second, no existing study has compared manual laterality in non-communication actions and in gestures considering tool-use activities (hypothesized to have facilitated the emergence of language capability in humans (e.g. Greenfield 1991; Higuchi et al. 2009; Forrester et al. 2013)) to assess the effect peculiar to communication on laterality.

To compare rigorously manual laterality between both functions (non-communication and communication) in order to assess the effect peculiar to the function other factors found to modulate hand preference must be taken into account. In fact, laterality in both functions could be modulated by several factors (e.g. see reviews McGrew & Marchant 1997; Meguerditchian et al. 2013) such as age, sex, hierarchy, and group[22]. The potential influence of the demographic factors age and sex has been typically the first to be examined but the results were heterogeneous among studies.

In the following paragraphs, we will briefly review current findings concerning the influence of socio-demographic factors on laterality.

Age

With regards to age, many studies in non-communication actions (e.g. chimpanzees: Boesch 1991; Hopkins 1994, 1995; Humle & Matsuzawa 2009; bonobos: Chapelain & Hogervorst 2009; Chapelain et al. 2011; Hopkins et al. 1993; Hopkins & de Waal 1995; orang-utans: Rogers & Kaplan, 1996; capuchin monkeys: Westergaard & Suomi 1993, 1994; lemurs: Ward

[22] 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).

et al. 1990; bushbabies: Milliken et al. 1991; marmosets: Hook & Rogers 2000) and in gestures (e.g. chimpanzees: Hobaiter & Byrne 2013; Hopkins & Leavens 1998; olive baboons: Meguerditchian & Vauclair 2006), have showed that direction and/or strength of hand preference becomes more salient with age suggesting that hand preference may be under control of maturation and/or the result of the amount of practice, learning and experience. However, age effects have not been consistently found across studies either in non-communication actions (e.g. chimpanzees: Hopkins 1993; Colell et al. 1995; bonobos: Colell et al. 1995; gorillas: Meguerditchian et al. 2010b; capuchin monkeys: Parr et al. 1997; olive baboons: Fagot et al. 1988; Vauclair & Fagot 1987; Meguerditchian & Vauclair 2009; rhesus monkeys Fagot et al. 1991; tamarins: Diamond & McGrew 1995) or in gestures (e.g. chimpanzees: Hopkins et al. 2005a; olive baboons: Meguerditchian & Vauclair 2009), making it difficult to draw firm conclusions concerning the influence of age.

Sex

Sex has also been shown to influence manual laterality, males' left-hand preference is higher than that of females in non-communication actions (e.g. chimpanzees: Byrne & Corp 2003; Corp & Byrne 2004; Hopkins et al. 2009; orang-utans: Rogers & Kaplan 1996; De Brazza's monkeys: Schweitzer et al. 2007; capuchin monkeys: e.g. Meunier & Vauclair 2007; squirrel monkeys: Meguerditchian et al. 2012a; see also Sommer & Kahn 2009 for a review). As far as we know, only two studies reported a sex effect in gestures with however contradicting results. Hopkins and Leavens (1998) found that male chimpanzees tended to be less right-handed than females while contrarily Hopkins and de Waal (1995) found that male bonobos were more right-handed than females. Nevertheless, some other authors did not find sex differences in manual laterality either in non-communication actions (e.g. chimpanzees: Hopkins 1995; olive baboons: Meguerditchian & Vauclair 2009, lemurs: Leliveld et al. 2008, see also reviews of Hook-Costigan & Rogers 1997; McGrew & Marchant 1997) or in gestures (e.g. chimpanzees: Hopkins et al. 2005a, 2005b; Meguerditchian et al. 2010a; Prieur et al. submitted; gorillas: Meguerditchian et al. 2010b; olive baboons: Meguerditchian & Vauclair 2006, 2009), leaving open the issue of the influence of sex on laterality.

Social status

The influence of individuals' hierarchical status on manual laterality has rarely been studied. Baraud and colleagues (2009) established that approach side and relative positions (transversal and vertical) were influenced by social rank: dominant mangabeys were approached more frequently from their left than from their right visual field and they left

conspecifics more often behind them. Prieur and colleagues (submitted) evidenced that subordinate chimpanzee initiators used globally more their right hand to communicate with conspecifics than initiators belonging to higher hierarchical rank. They hypothesized that stress produced by psychosocial factors would reduce subordinates' right-hemisphere activity (left-hand use) and thus increase the use of the right hand. Indeed, stress would reduce captive anoles' right-hemisphere activity for aggressive movements (Deckel 1998). Other studies evidenced that in non-social contexts rats presented a right-side bias at the population level in acute stress situations (e.g. electrified T-maze: Alonso et al. 1991; Castellano et al. 1987, 1989; tail suspension: Castellano et al. 1989). Given the lack of studies, these issues need to be explored further in primates.

Group

Finally besides individual characteristics such as age, sex and social status, the influence of belonging to a group and group differences in laterality have been considered in some previous studies. The social hypothesis of laterality (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009) postulates that social pressures may lead to the alignment of the direction of laterality at the group level for social-related behaviours. Concerning non-social behaviours (e.g. manipulations using a tool), Lonsdorf and Hopkins (2005) suggested that effects of genetic factors and/or social learning on laterality would explain variation of laterality patterns between groups. Concerning this group effect, no previous study showed any significant differences in hand preference between groups of captive chimpanzees (for the *tube task*: e.g. Hopkins et al. 2004; for human-directed FOOD BEG and POINTING (pooled data): Hopkins et al. 2005b; for human-directed CLAPPING: Meguerditchian et al. 2012; for THROWING directed towards both humans and conspecifics (pooled data): Hopkins et al. 2005a) and baboons (for HAND SLAP directed towards both humans and conspecifics (pooled data): Meguerditchian et al. 2011). Efforts must continue to compare groups to understand better the underlying mechanisms of population 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 caused by disparities between methodologies used to study manual asymmetries (e.g. see reviews of Cashmore et al. 2008; Cochet et al. 2013; Hopkins 2007; Meguerditchian et al. 2013; McGrew & Marchant 1997; Papademetriou et al. 2005) for instance the manual activities considered (spontaneous actions or experimental tasks, function

– for communication or not –, gestures directed towards humans and/or conspecifics), data collection and analyses (sample size, sociodemographic characteristics of the subjects, number of data points per subject, independence of data, statistical tests) as well as settings (captivity vs. wild). Another reason for disparities is that these studies did not use a comprehensive approach taking into account simultaneously multiple influential factors (including sociodemographic factors) and their interactions although it is a fundamental point to avoid biases yielding ambiguous results and also a mandatory requirement to assess the effect particular to the function (e.g. non-communication vs. communication). As far as we know, no previous study has investigated the effects of sociodemographic factors on laterality using this approach as well as considering several narrow categories of age (e.g. immature, adolescent, young and mature adult and elder) and hierarchical rank (e.g. dominant, intermediate and subordinate) which is also essential to better apprehend the effect particular to each modality of the considered sociodemographic variables.

Given the potential effects of the above-mentioned factors on manual laterality, a multifactorial investigation is mandatory to assess possible effects peculiar to the function (manipulation or communication). Thus the aim of the present study was to use such approach to compare manual laterality of tool-use in non-communication actions and in gestures in real-life social-ecological situations in one of our closest living congener chimpanzees (*Pan troglodytes*). Chimpanzees have become the predominant models for early hominoid behaviour because they also have a complex social structure (e.g. Aureli et al. 2008), communicate via rich gestural communication (Hobaiter & Byrne 2012; Pika & Mitani 2006), and show complex tool use (e.g. McGrew & Marchant 1997). We addressed the following two research questions and associated hypotheses:

(1) Is there a manual laterality bias at the population level in chimpanzees when examining first a non-communication tool use action similar to termite fishing (e.g. in wild chimpanzees: McGrew & Marchant 1992) and second each of five frequently expressed conspecific-directed gestures involving the use of a tool also reported in wild chimpanzees (e.g. Nishida et al. 2010). According to previous findings in chimpanzees for termite fishing (e.g. Bogart et al. 2012) and for gestures (e.g. Hopkins et al. 2012; Meguerditchian et al. 2013), we expected a marked laterality in tool-use at the population level (i.e. most subjects being lateralized) towards the left for the considered non-communication action and towards the right for the gestures.

(2) Is manual laterality in both functions modulated by individuals' sociodemographic characteristics? To investigate this question, we considered simultaneously the effects of age, sex, hierarchical rank, and group and possible interactions between these factors to overcome discrepancies and fragmented knowledge from previous studies. Based on literature on chimpanzees (e.g. Hopkins et al. 2009; Prieur et al. submitted), we predicted modulation by age, sex, and hierarchy but not by group.

Methods

Subjects and settings

Thirty-nine chimpanzees raised under semi-natural conditions were observed in three zoos: Leipzig Zoo (Germany), Beauval Zoo and La Palmyre Zoo (France). Individual characteristics are presented in Table 1. The age categories of the individuals were defined as follows: 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 & Leavens 1998 for captive chimpanzees). Zookeepers fed the studied subjects three to four times a day (depending on the zoos) with diverse types of fresh fruit, vegetables, branches with leaves, seeds, and raisins supplemented by primate pellets, vitamins and mineral drinks. Water was available *ad libitum*.

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Observation procedures

Observation data were collected between July and December 2013 at the Wolfgang Köhler Primate Research Center at the Leipzig Zoo, at the Beauval Zooparc, and La Palmyre zoo, resulting respectively in 333 hours, 198 hours and 174 hours of observation time per group/zoo. The observation and coding procedures are presented below. Data were collected using "sampling all occurrences of some behaviours" (Altmann 1974). These data correspond to gestures with and without a communication tool (Prieur et al. submitted) and to non-communication tool-use actions.

Coding procedure for the non-communication tool-use actions

Non-communication tool-use actions were observed and recorded during spontaneous daily activities. We focused on the use of a stick to obtain an out-of-reach goal. This tool manipulation requires precision similar to termite fishing (e.g. McGrew & Marchant 1992). In the three zoos, the 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 beyond its edge). For each tool manipulation, we recorded the hand (left or right) used by the subject to obtain the out-of-reach food.

Not all the chimpanzees expressed these behaviours: 25 (of which 6 immatures, 6 adolescents, 4 young adults, 5 mature adults and 4 elders; 9 males and 16 females) of the 39 studied chimpanzees performed a sufficient number of non-communication tool-use actions to be used for subsequent statistical analyses.

Coding procedure for conspecific-directed gestures involving a communication tool

In parallel with observations of spontaneous non-communication tool-use actions, we recorded spontaneous gestures performed by signallers in direction to a given conspecific and which involved a communication tool (Prieur et al. submitted). Only dyadic interactions between conspecifics were taken into account. For each interaction, we recorded (1) the type of gesture, (2) the hand (left or right) used by the signaller to communicate with a particular recipient, and (3) the identity of the signaller (i.e. its sociodemographic characteristics).

Following Pika's definition of a gesture (Pika 2008a, 2008b), we considered only intentionally produced gestures that (1) were used to initiate (but not to continue) a social interaction, (2) were mechanically ineffective (i.e. a gesture that "visibly lacks the mechanical force to bring about the reaction shown by the recipient, and also does not include any attempt to grab or extensively hold a body part of the other" Pollick & de Waal 2007, p. 8185), and (3) included hallmarks of intentional communication such as gazing at the recipient, gaze alternation, goal persistence, and/or response. 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 frequently enough to

enable a systematic comparison of hand-use with the non-communication tool-use actions. Other gestures involving a tool previously described in wild chimpanzees (Nishida et al. 2010) were also observed in the three study groups, but represented extreme rare cases. 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 Table 2.

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Data requirements and independence

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. A requirement for a hand to be recorded was that both hands of the initiator were free and symmetrically positioned with respect to its body midline before the action (non-communication or communication), without any environmental factors that could potentially influence the use of one hand (e.g. being close to a wall/bush/tree). Data were recorded when an action was expressed either singly or in bouts (e.g. Marchant & McGrew 1991; Byrne & Byrne 1991). Only the first manual action of a sequence of bouts was recorded. The determination of the end of an action or of a bout of actions was based on precise criteria: the subject's hand returned to its initial position (Meguerditchian et al. 2010a) or switched to another non-communication activity (e.g. forage) or when an incident (e.g. stumble) occurred that might influence the use of one hand (Hopkins & de Waal 1995; Hopkins et al. 2001; McGrew & Marchant 2001; Harisson & Nystrom 2010). To ensure statistical independence of data, a change in hand activity must last more than three seconds before another action could be recorded (Morris et al. 1993; Hopkins & de Waal 1995).

Identification of hierarchical rank

In addition to individual demographic characteristics (age, sex, zoo), we considered social status. Hierarchical ranks were determined in our previous chimpanzees' study (Prieur et al. submitted). They were based on the analysis of agonistic interactions (Pollick & de Waal 2007) within dyads with clear aggressor and recipient of the threat (Langbein & 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 interactions included 16 conspecific-directed mechanically ineffective gestures (BEAT BODY, CLAP HAND, HIT WITH OBJECT, DRAG OBJECT, HAND ON, KICK, PUNCH, PUSH, PUT OBJECT ON HEAD/BACK, RAISE ARM, REACH, SHAKE OBJECT, THROW OBJECT, SLAP FOOT, SLAP HAND and SLAP) and two conspecific-directed mechanically effective gestures: GRAB and PUSH (mechanical effective version) (Pika et al. 2005a).

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'* (de Vries 1995) using MatMan 1.1 (Noldus Information Technology, Wageningen, Netherlands). 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).

Statistical analysis

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

Descriptive statistics of laterality at the individual and population level

To enable subsequent statistical analyses using binominal test (Siegel & Castellan 1988), we only used data for behaviours (conspecific-directed gestures involving a tool and the non-communication tool-use actions considered) that had been performed at least six times each by a least six individuals (Chapelain 2010).

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. 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 (ABSHI). This procedure is similar to that used previous authors (e.g. Harris & Carlson 1993; Hopkins 1995).

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 lateralized and non-lateralized individuals was assessed for each behaviour using the binomial test. For each behaviour when at least six subjects were lateralized, we assessed population-level bias in the number of right-handers and left-handers using the binomial test. For each behaviour, population-level bias of hand use was evaluated using the one-sample two-sided Student's t-test on the HI values of all the individuals when the distribution of HI data was normal (Shapiro-Wilk normality test). It has been suggested that sample size can influence laterality in direction and strength (McGrew & 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.

Generalized 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 tested the effects of these functional and individual variables on laterality using generalized linear mixed model (GLMM) for binary data (logistic regression) with hand use as the dependent variable. Initiators' identity was considered a random variable to prevent pseudo-replication due to repeated observations (Waller et al. 2013) (see Table 3 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 into one category noted "C Tool use". This regrouping of four visual gestures and one tactile gesture was justified by Prieur and colleagues' (submitted) results that did not put in evidence that sensory modality modulated laterality of gestures involving use of a communication tool. The fixed variables were thus individual sociodemographic characteristics (age, sex, hierarchy, and zoo) and "Tool use activity" (two modalities: "C Tool use" (gestures involving a tool) and "NC Tool use" (non-communication tool-use actions)) for comparisons between tool-use in gestures and in non-communication actions. All possible interactions between fixed variables were included at the beginning of the iterative model selection.

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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 & 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 Tukeys' HSD test and differences were calculated between LSmeans (lsmeans package).

Results

Overall, we recorded 6647 occurrences of gestures involving a communication tool and 1689 occurrences of non-communication tool-use actions respectively for 39 and 25 chimpanzees during 705h of observations. After having applied the statistical criterion required for binomial tests (Siegel & Castellan 1988), 6567 occurrences of gestures and 1678 occurrences of non-communication tool-use actions were retained for the following descriptive statistics and related analyses.

Manual laterality in communication and non-communication tool uses at the population level

To investigate whether a manual laterality bias is observed at the population level, we analyzed it for the non-communication tool-use actions considered as well as for each of the five conspecific-directed gestures involving a communication tool considered separately (see details in Table 4). The associated mean number of occurrences per individual was 172.74 for the five gestures (min = 6, max = 841; SD = 236.53) and 88.32 for the non-communication tool-use actions (min = 14, max = 278; SD = 72.29).

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Concerning gestures involving a tool, significantly more subjects were non-lateralized than lateralized only for DRAG OBJECT (Binomial test: $P = 0.023$; detailed in Table 4). The average percentage of non-lateralized individuals for the five gestures was 57.31% (min = 41.67%, max = 84.62%, SD = 16.57). No statistically significant differences could be evidenced between the numbers of non-lateralized and lateralized subjects for non-communication tool-use actions (Binomial test: $P = 0.167$); the percentage of non-lateralized individuals was 31.58%.

There were significantly more right-handed than left-handed subjects for one gesture SHAKE OBJECT over the two presenting sufficient lateralized subjects for testing (binomial test, Table 4). Considering HI as a continuum, each of the five gestures presented a significant right-hand bias at the population level (one-sample two-sided t-test, Table 4). The average Mean HI for the five gestures was 0.35 (min = 0.26, max = 0.47; SD = 0.09) and the average Mean ABSHI was 0.42 (min = 0.28, max = 0.60; SD = 0.12). No population-level bias in the direction of hand preference could be evidenced for non-communication tool-use actions (Mean HI = 0.22; Mean ABSHI = 0.54), (one-sample two-sided t-test, Table 4).

No significant effect of the number of data points per individual on the HI and ABSHI values for each of the five conspecific-directed gestures involving a tool or for non-communication tool-use actions could be evidenced (Spearman correlation test, Appendix Table A1)

Factors influencing laterality and their interactions

To assess whether, and how, function – communication vs. non-communication – impacted subjects' laterality in tool-use activities according to the subjects' characteristics,

(1) we compared right-hand use between non-communication tool-use actions (i.e. tool manipulations using a stick to obtain an out-of-reach goal) and a category regrouping the five gestures involving a tool, taking into account subjects' sociodemographic characteristics (i.e. age, sex, hierarchical rank, and zoo), and

(2) we assessed the influence of subjects' characteristics on right-hand use in both gestures and non-communication actions. The analysis of deviance results corresponding to the best GLMM model is presented in Table 5. No significant fixed variable was accounted for since the variable was involved in significant interactions with other variables. Only significant interactions were considered. The results of post-hoc multiple comparisons are

presented in Appendix Tables A2-A5. For clarity, significant and trend p-values are mentioned in the text below but all p-values can be found in Tables A2-A5.

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Influence of communication in tool-use activity in relation to subjects' age class. We found a significant interaction between tool-use activity (communication *vs*. non-communication) and initiators' age class (Analysis of deviance, Table 5). Laterality patterns differed between age classes (see Table A2 for post-hoc comparisons, 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 reverse pattern was found for immatures who were more right-handed in gestures than in non-communication actions (Tukey test: $P < 0.0001$). No significant communication effect was found for elders (Tukey test: $P = 1$). Moreover, we found significant differences between age classes in both communication and non-communication tool uses (see Table A2 for post-hoc comparisons, Fig 1b). For gestures, elders were less right-handed than all the younger age classes: this difference reached the significance level for adolescents, young and mature adults (Tukey test: adolescents: $P = 0.035$; young adults: $P = 0.017$; mature adults: $P = 0.002$), but not for immatures ($P = 0.148$). No significant differences appeared between the other age classes (all $P > 0.90$). For non-communication actions, both elders and immatures were significantly less right-handed than adolescents, young and mature adults (Tukey test: all $P < 0.0001$). Immatures were also less right-handed than elders (Tukey test: $P = 0.006$). The other age classes, adolescents, young and mature adults, presented very similar levels of laterality in non-communication actions (all $P > 0.20$).

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Influence of communication in tool-use activity in relation to sex. We found a significant interaction between tool-use activity (communication *vs*. non-communication) and initiators' sex (Analysis of deviance, Table 5). Similar patterns of laterality were found for males and females (see Table A3 for post-hoc comparisons, Fig. 2). Male initiators were significantly more right-handed when using a tool in non-communication actions than in

gestures (Tukey test: $P = 0.039$). A similar, less pronounced tendency was observed for females (Tukey test: $P = 0.079$). No evidence of significant between-sex differences was found whatever the function (Tukey test: all $P > 0.30$).

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Influence of communication in tool-use activity in relation to hierarchical rank. We found a significant interaction between tool-use activity (communication vs. non-communication) and initiators' hierarchical rank (Analysis of deviance, Table 5). Patterns of laterality differed with social status (see Table A4 for post-hoc comparisons, 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 in non-communication actions than in gestures (Tukey test: $P < 0.0001$). There was no evidence of such communication effect in tool-use activity for intermediate initiators (Tukey test: $P = 0.599$). Between-rank comparisons revealed no evidence of a significant influence of initiator's hierarchical status on initiators' right-hand use in gestures (Tukey test: all $P = 1$); all ranks had very similar level of laterality in gestural communication. For non-communication actions however, right-hand use increased significantly with decreasing hierarchical rank: dominants were less right-handed than intermediates (Tukey test: $P < 0.0001$) that were less right-handed than subordinates (Tukey test: $P < 0.0001$).

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Influence of communication in tool-use activity in relation to group (zoo). We found a significant interaction between tool-use activity (communication vs. non-communication) and initiators' zoo (Analysis of deviance, Table 5). There was no evidence of significant communication effect in tool-use activity whatever the zoo (Tukey test: Leipzig, Palmyre, both $P > 0.10$) (see Table A5 for post-hoc comparisons). Only initiators at Beauval zoo tended to be more right-handed when using a tool in a non-communication actions than in gestures (Tukey test: $P = 0.064$). When comparing data for the three zoos, no evidence of an influence of the zoo was found whatever the function (Tukey test: all $P > 0.20$). All together, these results indicated that the influence of group/zoo was limited.

Discussion

Our study compared chimpanzees' manual laterality in the context of tool use in non-communication actions and in intraspecific gestures in order to evaluate first, whether manual laterality was observed at the population level for the non-communication tool use actions and each of the five conspecific-directed gestures involving a tool; and second, whether the expected differences of chimpanzees' manual laterality between gestures and non-communication actions (i.e. greater right-hand use in communication than in manipulation) are modulated by individual sociodemographic characteristics. Considering laterality on a continuum (e.g. McGrew & Marchant 1997), evidence of a population-level right-hand use bias was found for each of the five conspecific-directed gestures involving a tool but not for non-communication tool-use actions. Moreover, our multivariate study showed that manual laterality in both functions was influenced by individuals' characteristics. Laterality of dominant and immature initiators was directed more to the right in gestures than in non-communication actions. On the contrary, subordinates, adolescents, young and mature adults as well as males were more right-handed in non-communication actions than in gestures. No differences between functions were found for intermediates, elders, females as well as for the three groups/zoos.

In the following paragraph, we will discuss our findings in relation to the analysis of lateral bias in hand use at the population level.

Manual laterality in tool use in non-communication actions and in gestures at the population level

For the non-communication tool use actions, we did not evidence a population-level bias. Our results are consistent with Hopkins and colleagues' (2009) study of captive chimpanzees using a tool-use task designed to simulate termite fishing. Contrarily, studies on laterality in termite fishing by two wild chimpanzees communities, Gombe in Tanzania (McGrew & Marchant 1992, 1996, 1999; Lonsdorf & Hopkins 2005) and Fongoli in Senegal (Bogart et al. 2012) revealed a left-hand bias at the population level.

The difference in hand preference between the present study and these studies may be the consequence of genetic factors and/or social learning on laterality as suggested by Lonsdorf and Hopkins (2005) to explain task-specific variation in direction of laterality

between groups of wild chimpanzees in tool-use actions. This divergence of results could also be due to a "difference in haptic and sensory requirements during insertion and extraction" (Hopkins et al. 2009) between our non-communication tool use actions and termite fishing in the wild.

For gestures involving a communication tool, we found a right-hand bias at the population level. This bias has been reported previously for the Budongo chimpanzee community, Uganda for a category of object-manipulation gestures directed towards conspecifics combining OBJECT SHAKE and OBJECT MOVE (Hobaiter & Byrne 2013). Our results are also in agreement with the studies of chimpanzees in captivity for THROWING directed towards humans (Hopkins et al. 1993) and towards both humans and conspecifics (pooled data) (Hopkins et al. 2005a). This bias has also been reported for chimpanzees and baboons for conspecific-directed gestures not involving use of a tool (e.g. chimpanzees for a category of species-typical gestures combining THREAT, EXTEND ARM and HAND SLAP: Meguerditchian et al. 2010a; baboons for HAND SLAP: Meguerditchian & Vauclair 2006; Meguerditchian et al. 2011). To sum up, the present study on chimpanzees' gestures involving a communication tool provides additional support to previous findings in favour of a predominant implication of the left cerebral hemisphere in the gestural communication system of some non-human primates.

The reliability of our findings was overall enhanced by the absence of an effect of the number of data points per subject on the HI and ABSHI values found for non-communication tool-use actions and for each of the five intraspecific gestures.

Several factors have been suggested to explain variation between social groups: first, genetic factors and/or social learning for laterality in non-communication tool use actions (Lonsdorf & Hopkins 2005); second, social pressures for laterality in communication function, (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009). If these explanations are true, then we would have expected to find differences on manual laterality between groups in both function (non-communication and communication). However, such differences were not found in our observations. This absence of group effect on manual laterality in both functions is congruent with previous studies of captive chimpanzees (for the *tube task*: Hopkins et al. 2004; for THROWING directed towards both humans and conspecifics (pooled data): Hopkins et al. 2005a; for human-directed FOOD BEG and POINTING (pooled data): Hopkins et al. 2005b; for human-directed CLAPPING Meguerditchian et al. 2012) and of captive baboons (for HAND SLAP directed towards both

humans and conspecifics (pooled data): Meguerditchian et al. 2011). Concerning the three study groups, our results did not support either an effect of genetic factors and/or social learning on laterality in non-communication actions, or an effect of social pressures on laterality in communication function. However, manual laterality in tool use in both functions was modulated differently in relation to sociodemographic factors. Evidence of these modulations is discussed below.

Manual laterality in tool use in non-communication and communication functions: modulation by sociodemographic factors

As far as we know, the present study is the first to compare non-human primates' manual laterality in non-communication and communication functions focusing on tool-use activities (hypothesized to have facilitated the emergence of language capability in humans (e.g. Greenfield 1991; Higuchi et al. 2009; Forrester et al. 2013). Our results concerning the effect peculiar to the function 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 (pooled data) contrary to our study which only considered intraspecific communication. To discuss our results concerning the effect peculiar 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.

Influence of initiator's hierarchical rank

We evidenced an influence of hierarchical status on right-hand use in a non-communication action, namely dominants were less right-handed than intermediates who were less right-handed than subordinates. To our knowledge, this is the first evidence of a hierarchical rank effect on manual laterality in non-communication actions. The observed increase in right-hand use with decreasing hierarchical rank in the context of food access may be associated to a higher level of psychosocial stress. In fact, Sapolky (2002) evidenced that baboons under stress as in a context of food access (Creel et al. 2013) produced high levels of glucocorticoids enabling them to optimize energy availability. Most low-ranking social animals usually maintain a higher level of glucorticoids than high-ranking animals (Creel et

al. 2001). Recently this relationship between captive chimpanzees' level of glucorticoids and social rank has been investigated. Markham and colleagues (2014) evidenced that lower-ranking lactating females had higher level of faecal glucocorticoid metabolites than higher-ranking lactating females. They suggested that this variation could be the consequence of psychosocial stress because lower-ranking females received more male aggression than higher-ranking females. As mentioned by Creel and colleagues (1996), the increasing intensity of psychosocial stress would be more important in captivity because of spatial constraints. Deckel (1998) revealed a relationship between stress and brain activity, stress decreased captive anoles' right-hemisphere activity for aggressive movements during intraspecific interactions. Based on a study of captive chimpanzees' intraspecific gestural laterality, Prieur and colleagues (submitted) recently evidenced that subordinate signallers used their right hand more than did higher ranking signallers (i.e. intermediate and dominant). Inspired by Deckel (1998), these authors suggested that the psychosocial stress of subordinate chimpanzees would inhibit the activity of their right hemisphere (mostly associated with left-hand movements as for humans: Serrien 2009). This assumption is supported by studies of rats and humans. Indeed, rats have a right-side bias at the population level in acute stress situations (e.g. electrified T-maze: Alonso et al. 1991; Castellano et al. 1987, 1989; tail suspension: Castellano et al. 1989). Rohlfs and Ramirez (2006) reviewed that stressed humans produced several neurochemical changes causing structural and functional alterations in their right hemisphere: inhibition of dendritic branching and reduction of brain nucleic acid synthesis which leads to axonal death (Joseph 1994; Schore 1997) as well as increase of dopamine (Bertollucci-D'Angio et al. 1990) inducing neurotoxic inhibition of mitochondrial respiration and defective energy metabolism (Ben-Shachar et al. 1994). 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 subordinates and to a lesser extent intermediates. This would be particularly the case in our study in the context of food access known to induce stress (Creel et al. 2013).

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 result is thus coherent with Prieur and colleagues' (submitted) study reporting the absence of a hierarchical rank effect for visual gestures but not for tactile gestures. Laterality of tactile gestures could be affected by psychosocial stress potentially because these gestures imply close proximity between partners. 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. They were thus potentially less associated to psychosocial stress. This would explain the observed absence of any effect of hierarchical rank on laterality for the five gestures.

Influence of initiator's age class

Our comparisons between age classes in both non-communication actions and gestures indicated that elders were less right-handed than adolescents, young and mature adults. This decrease in right-hand use with age has been documented for humans (Kalisch et al. 2006). A reason may be that physical limitation and lower activity (Hughes et al. 1997; Schut 1998; Ranganathan et al. 2001) as well as lower sociality associated with aging would decrease practice-based performance of the right hand that would thus converge towards use of the left hand. A similar effect for chimpanzees may explain the elders' shift towards ambidexterity observed. As far as we know, this is the first evidence of a possible senescence effect on manual laterality of non-human primates in both non-communication actions and gestures.

Concerning non-communication actions, immatures were much less right-handed than adolescents, young and mature adults and elders. This move towards the right with age until the shift in elderly in tool-use actions has also been showed for chimpanzees' nut-cracking (Boesch 1991) as well as for capuchin monkeys reaching for food and sponging (Westergaard & Suomi 1993) and use of a probing tool (Westergaard & Suomi 1994). Five of our six immatures belonged to the subordinate class. 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. As mentioned by De Bellis (2005) humans' neural circuits that deal with stress are particularly plastic during early childhood, experience shaping them progressively. Therefore, possibly immature chimpanzees' motor and cognitive abilities that control stress would be less developed and thus less effective than that of older subjects. We assume that this lower efficacy would not allow the increase of right-hand use found for older subordinates in the context of food access. Moreover, the potential lower efficacy of immatures' motor and cognitive abilities to control stress may be combined with an effect of the haptic demand of the task (particularly pronounced for subordinates) to explain their particularly low level of right-hand use in non-communication tool-use actions. The fact that during our observations dominants were generally the first individuals of the group to obtain access to a palatable food source (out-of-

reach food such as pellets inside a box) and to extract it by using a stick must be mentioned. They could obtain 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 observation). Lacreuse and Fragaszy (1999) and Spinozzi and Cacchiarelli (2000) showed that, for the processing of haptic information during visual-tactile tasks by tufted capuchin monkeys, a greater involvement of the right cerebral hemisphere (i.e. left hand) would explain the particular low level of right-hand use by immatures for non-communication tool use.

Concerning gestures involving a tool immatures' laterality pattern did not differ statistically from that of older subjects. Except for elders, our results showed an absence of differences between age classes in gestures. This is in accordance with Hopkins and colleagues' (2005b) results for THROWING directed towards both humans and conspecifics (pooled data); this, to our knowledge, is the only study investigating age effects on laterality in gestural communication involving use of a tool. According to the literature on gestural communication without a tool, age effect on laterality, however, remains unclear. Some studies did not detect any age effect (chimpanzees, for human-directed FOOD BEG and POINTING (pooled data): Hopkins et al. 2005b; baboons, for human-directed FOOD BEG: Meguerditchian & Vauclair 2009) whereas other studies found that right direction in hand preference increased with age (wild chimpanzees, for 20 gesture types (pooled data): Hobaiter & Byrne 2013; captive chimpanzees, for human-directed FOOD BEG and POINTING (pooled data): Hopkins & Leavens 1998; baboons, for HAND SLAP directed towards both humans and conspecifics (pooled data): Meguerditchian & Vauclair 2006).

Influence of initiator's sex

Between-sex comparisons did not reveal any evidence of sex differences in initiator's right-hand use either in non-communication actions or in gestures. This is in accordance with most studies that did not find a sex effect on manual laterality in both functions including studies of captive chimpanzees (e.g. for the *tube task*: Hopkins et al. 2003; for FOOD BEG and POINTING (pooled data): Hopkins et al. 2005a; for THROWING directed towards both humans and conspecifics (pooled data): Hopkins et al. 2005b; for a category of species-typical gestures combining THREAT, EXTEND ARM and HAND SLAP: Meguerditchian et al. 2010a) and captive baboons (for grasping food and for the *tube task*: Vauclair et al. 2005; for FOOD BEG: Meguerditchian & Vauclair 2009; for HAND SLAP: Meguerditchian & Vauclair 2006) (see also

review by McGrew & Marchant 1997). 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 review by Meguerditchian et al. 2013). The difference between our results and Hopkins and colleagues' (2009) results could be explained by the above-mentioned effects of genetic factors and/or social learning on laterality in non-communication tool use actions by chimpanzees (Lonsdorf & Hopkins 2005). In addition, the potential influence of hormones on laterality has rarely been studied in non-human primates but studies suggested that circulating hormones could affect rhesus monkeys' laterality by increasing or decreasing its strength (Drea et al. 1995; Westergaard et al. 2000) or modifying its direction (Westergaard & Lussier 1999; Westergaard et al. 2000, 2003). Further research is required to explore the influence of sex on manual laterality and its determinants.

Influence of the function: non-communication vs. communication

After having discussed the respective influences of sociodemographic factors on manual laterality in tool-use in both functions, we can now understand better the effect of function (non-communication vs. communication) on laterality. Considering this effect, 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 evidence of a difference was found for intermediates, elders, females as well as for the three groups/zoos.

With regard to dominants, they may be less subject to psychosocial stress to access food than lower-ranking subjects (i.e. intermediates and subordinates). Therefore, we assume that the difference observed for dominants may represent at the best the effect of function that would be: gestures with a tool elicit greater right-hand use than manipulations with a tool. With regard to subordinates, however, they may be particularly subject to psychosocial stress to access food, stress that has been suggested to induce increase of right-hand use. This increase would lead to a converse effect of function on subordinates (more right-hand use in manipulations than in gestures with a tool).

The difference observed for immatures, predominantly subordinates (five of the six immatures), concerning function could be explained 1) by a weaker effect of psychosocial stress possibly due to less developed and thus less effective motor and cognitive abilities and 2) by the specific sensorimotor requirements of the tool task considered (i.e. haptic demands of the task) associated with lower-ranking individuals (see above the explanation in the

discussion about age effects on laterality in non-communication tool-use actions). Only one of the 15 adolescent, young and mature adult age class subjects was a subordinate. The greater right-hand use observed in non-communication actions than in gestures may be attributed to the absence of haptic constraints combined with age-related experience that has already been mentioned to reinforce right direction in hand preference (e.g. Boesch 1991; Westergaard & Suomi 1993, 1994).

Males' and females' use of their right hand was greater in non-communication actions than in gestures. This difference between functions was significant for males whereas only a trend was found for females. Two non-exclusive reasons might explain the observed difference of the function effect between males and females. First, this may be the consequence of differences in practice and/or learning, factors already found 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 study males were more experienced than the females for practicing non-communication actions, either by having started to practice earlier than females and/or having practiced them more frequently. This hypothesis is supported by Lorincz and Fabre-Thorpe's (1996) report evidencing a shift of cats' paw use towards the right after practice of a visual motor task. Second, circulating hormones (including testosterone and cortisol) influence the direction and the strength of rhesus monkeys' laterality (Drea et al. 1995; Westergaard & Lussier 1999; Westergaard et al. 2000, 2003). Further studies are necessary to understand the causes of sex differences.

As previously mentioned, existing studies concerning the effect of function (non-communication vs. communication) have compared laterality in manipulations and in gestures not involving a tool (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), olive baboons (Meguerditchian & Vauclair 2006; Meguerditchian et al. 2011; Meguerditchian & Vauclair 2009; Meunier et al. 2012), as well as by young children (Bates et al. 1986; Bonvillian et al. 1997; Vauclair & Imbault 2009; Cochet et al. 2011; Esseily et al. 2011; Meunier et al. 2012). As these studies did not compare laterality for tool-

use in both functions and did not consider only gestures directed towards conspecifics, their results cannot be rigorously compared to ours. Nevertheless, a link is possible with our study. Their common conclusion (greater right-hand use for communication than for non-communication) can be related to the methodology used in the studies concerning non-human primates. This can be explained by our results concerning hierarchical effect on laterality of tool-use manipulations by looking closer at their methodology. 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 of 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 presumed to be less stressed psychosocially than when they were not isolated (as in our study). They would thus have used less their right hand in 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 & Vauclair 2009). This hypothesis is in agreement with magnetic resonance imaging studies that show that chimpanzees' right-hand preference for FOOD BEG (Taglialatela et al. 2006, 2008) and CLAPPING (Meguerditchian et al. 2012) was linked to morphological left asymmetries in the inferior frontal gyrus (the homolog of the human Broca's area) whereas hand preference for non-communication manual actions (i.e. *tube task*) was not associated with asymmetries of any homologous language areas but with asymmetries of the primary motor cortex (Hopkins & Cantalupo, 2004).

Conclusion

The aim of our study was to compare chimpanzees' manual laterality for tool use in non-communication actions and intraspecific gestures. Our findings show first the intertwinement effect 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. Second, our findings concerning dominant chimpanzees, who may be free from psychosocial stress and haptic constraints in a food access context (contrary to subordinates and intermediates), suggest that tool-use in gestures would be governed more by the left cerebral hemisphere than tool-use in non-communication actions. Our results support the hypothesis that manipulation and communication components do not share the same lateralized cerebral system in some primates. Although the use of a tool in non-communication actions elicited strong laterality (in its direction and particularly its 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) in the sense that complex temporal sequences with high sensorimotor requirements of tool-use activities in both functions induce a strong right-hand use. However, it would be necessary to test these three hypotheses on other spontaneous tool use actions such as wadge-dipping (Boesch 1991). 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 manifestation of hemispheric specialization in humans that are right-handedness for manipulation and left-hemispheric specialization for language. In addition, our study underlines the need to explore laterality considering as many potentially influential factors as possible to ensure a reliable comparative approach between studies and species. Application of such approach will help us shed light on factors that govern handedness and possibly understand apparent inconsistencies between existing studies. It will also help stimulate the thinking about models explaining the expression and evolution of handedness (e.g. Annett 1985; Crow 2004; Geschwind & Galaburda 1985; Hopkins 2004; Laland et al. 1995; Levy & Nagylaki 1972; MacNeilage et al. 1987; McManus 1991). Furthermore, as previously pointed out in the existing literature, investigating human and non-human primates' intraspecific gestural laterality in real-life situations appears to be necessary to improve our comprehension of the evolutionary origins of language.

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Table notes

Table 1. F: Female; M: Male

Table 2. Conspecific-directed gestures are organized by sensory modality (four visual gestures then one tactile gesture) and for each sensory modality listed by alphabetic order. 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.

Table 3. C Tool use: Communication tool use; NC Tool use: Non-communication tool use

Table 4. Conspecific-directed gestures are listed by sensory modality and for each sensory modality in relation to increasing Mean HI values. N total: number of individuals who performed at least once the given manual activity; Data points total: total number of data points; N analyzed: 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 analyzed 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 analyzed 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 analyzed individuals; Mean ABSHI: Mean Absolute value of Handedness Index score of N analyzed individuals. Significant results are in bold.

Table 5. χ^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 A1. Conspecific-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. Significant results are in bold.

Table A2. 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 A3. 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 A4. 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 A5. 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 1. Individual characteristics of the study sample

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

Table 2. Gestural repertoire and detailed description

Gesture	Description	References
DRAG OBJECT	Subject pulls an object (e.g. branch) on the ground with one hand towards another subject	Nishida et al. (1999, 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 (1992, 1998)
THROW OBJECT *	Subject sends an object (e.g. branch) through the air with one hand towards another subject	Hohmann & Fruth (2003a, b)
HIT WITH OBJECT *	Subject clubs another subject with object (e.g. branch) held in one hand	Nishida et al. (1999, 2010)

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

Name	Type
Dependent variable	
Hand use	Dichotomous (Left/Right)
Fixed variables	
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)
Random variable	
Initiator's identity	Nominal

Table 4. 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	RH	B test LH vs. RH	Mean HI	Shapiro test	t-test		Mean ABSHI
Conspecific-directed gesture															
DRAG OBJECT	Visual	22	510	13	488	11	**0.023**	0	2	i.l.	0.257	0.845	t=0.256	***P*=0.0005**	0.282
PUT OBJECT ON HEAD/BACK	Visual	20	396	11	386	6	1	0	5	i.l.	0.302	0.591	t=0.302	***P*=0.024**	0.398
SHAKE OBJECT	Visual	39	5097	38	5096	18	0.871	1	19	**0**	0.314	0.340	t=0.314	***P*<0.0001**	0.352
THROW OBJECT	Visual	26	376	12	348	5	0.774	1	6	0.125	0.411	0.056	t=0.411	***P*=0.021**	0.598
HIT WITH OBJECT	Tactile	23	268	12	249	7	0.774	0	5	i.l.	0.466	0.745	t=0.466	***P*=0.0004**	0.491
Non-communication tool-use actions	–	25	1689	19	1678	6	0.167	4	9	0.267	0.224	0.221	t=0.224	*P*=0.130	0.540

Table 5. Analysis of deviance (Type II Wald chi-square tests) for the best GLMM model

Fixed terms and associated interactions	χ^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	**0.031**
Tool-use activity × Initiator's age class	46.003	4	**2.459e-09**
Tool-use activity × Initiator's sex	4.268	1	**0.039**
Tool-use activity × Initiator's hierarchical rank	43.253	2	**4.054e-10**

Table A1. 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		
Conspecific-directed gesture						
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
Non-communication tool-use actions	rs = 0.3358	*P* = 0.160	*N* = 19	rs = 0.1987	*P* = 0.4149	*N* = 19

Table A2. 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	**0.002**
C Tool use,Eld.	-	C Tool use,Y.adu.	-1.073	0.306	-3.504	**0.017**
C Tool use,Eld.	-	C Tool use,Ado.	-0.841	0.256	-3.284	**0.035**
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	**<0.0001**
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	**<0.0001**
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	**0.0003**
C Tool use,Y.adu.	-	NC Tool use,Y.adu.	-3.085	0.613	-5.032	**<0.0001**
NC Tool use,Eld.	-	NC Tool use,M.adu.	-5.482	0.853	-6.428	**<0.0001**
NC Tool use,Eld.	-	NC Tool use,Y.adu.	-4.441	0.699	-6.357	**<0.0001**
NC Tool use,Eld.	-	NC Tool use,Ado.	-4.165	0.673	-6.189	**<0.0001**
NC Tool use,Eld.	-	NC Tool use,Imm.	2.731	0.721	3.786	**0.006**
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	**<0.0001**
NC Tool use,Imm.	-	NC Tool use,M.adu.	-8.213	1.271	-6.462	**<0.0001**
NC Tool use,Imm.	-	NC Tool use,Y.adu.	-7.172	1.058	-6.779	**<0.0001**
NC Tool use,M.adu.	-	NC Tool use,Y.adu.	1.041	0.503	2.070	0.549

Table A3. 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	**0.039**
NC Tool use,F	-	NC Tool use,M	-0.924	0.582	-1.587	0.386

Table A4. 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	**<0.0001**
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	**<0.0001**
NC Tool use,Dominant	-	NC Tool use,Intermediate.	-2.739	0.565	-4.851	**<0.0001**
NC Tool use,Dominant	-	NC Tool use,Subordinate.	-6.451	0.982	-6.568	**<0.0001**
NC Tool use,Intermediate.	-	NC Tool use,Subordinate.	-3.712	0.705	-5.265	**<0.0001**

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

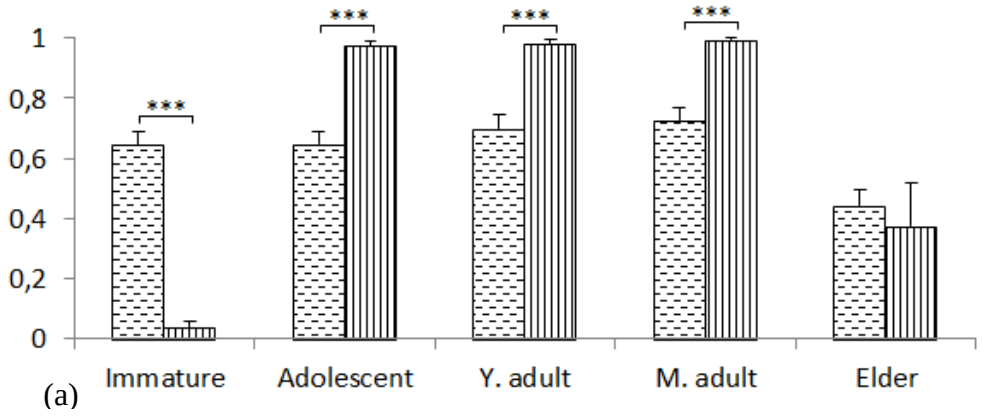
Figure captions

Figure 1. Adjusted probability (± 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: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Figure 2. Adjusted probability (± 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: $*P < 0.05$.

Figure 3. Adjusted probability (± 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: $***P < 0.001$.

Figure 1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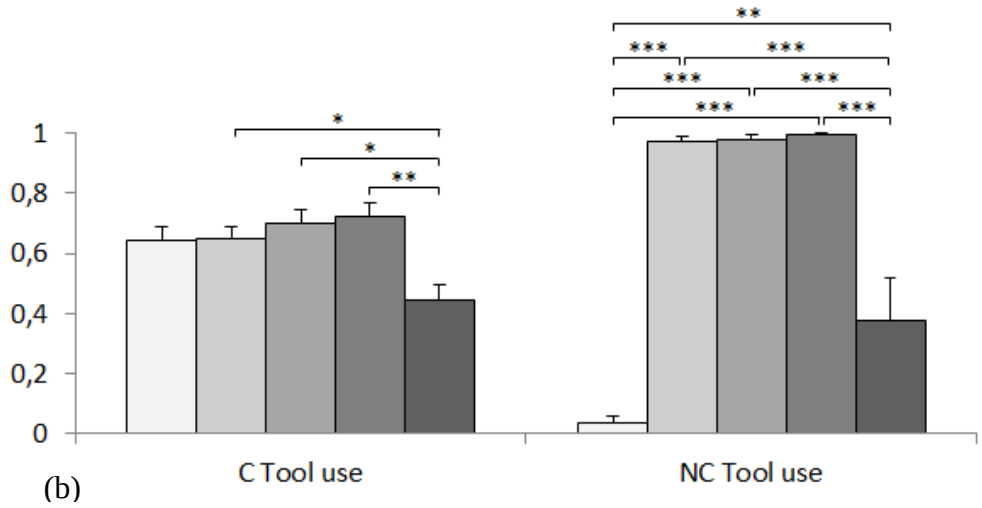
Immature
Adolescent
Y. adult
M. adult
Elder

(a)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(b)

Figure 2

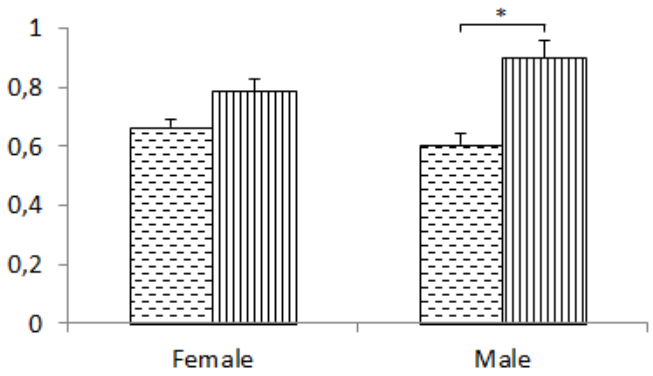
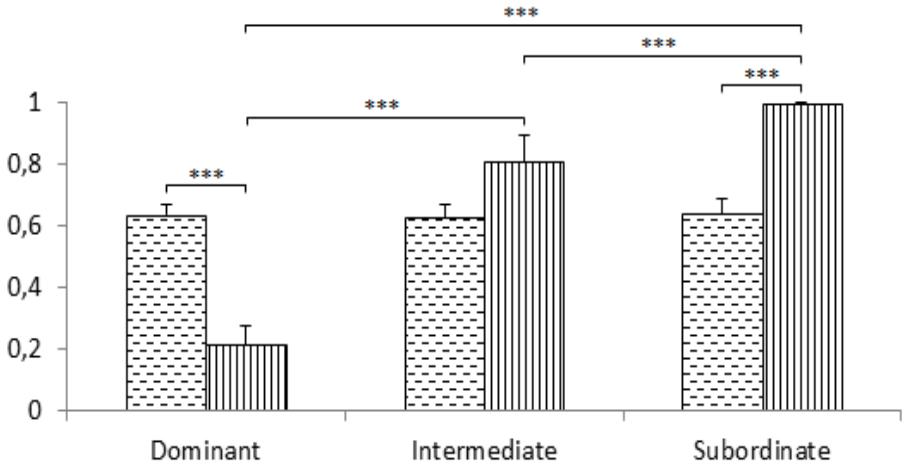


Figure 3



CHAPTER 5

General discussion and Conclusion

General discussion

Studying gestural laterality under socio-ecologically relevant conditions close to conditions where natural selection acted is of particular interest in an evolutionary perspective. Thus, investigations must consider contexts where subjects interact with conspecifics in suitable environments: in the wild and/or in favourable captive conditions (when naturalization of enclosures is optimal and social groups include many subjects). As far as we know, only few studies investigated laterality in of purely intraspecific gestures of non-human primates (chimpanzees: Fletcher & Weghorst 2005; Meguerditchian et al. 2010a; Hobaiter & Byrne 2013; bonobos: Chapelain 2010; olive baboons: Meguerditchian & Vauclair 2006). Moreover, few studies have compared manual laterality for manipulation and for gestural communication (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. 2013b; olive baboons: Meguerditchian & Vauclair 2006, Meguerditchian et al. 2011; Meguerditchian & Vauclair 2009; Meunier et al. 2012; young children: Bates et al. 1986; Bonvillian et al. 1997; Vauclair & Imbault 2009; Cochet et al. 2011; Esseily et al. 2011; Meunier et al. 2012). The comparisons in these studies considered gestures directed towards humans or both humans and conspecifics (pooled data) but never purely intraspecific gestures.

To our knowledge, no study has previously assessed manual laterality:

1. by taking simultaneously into account the potential influence of multiple factors and their interactions, an essential point to avoid biases yielding ambiguous results and also a mandatory requirement to assess effects particular to the function (e.g. non-communication vs. communication),

2. by investigating the effects of sociodemographic factors on laterality considering several narrow categories of age (e.g. immature, adolescent, young and mature adult and elder) and hierarchical rank (e.g. dominant, intermediate and subordinate), an essential point to apprehend better effects particular to each modality of the sociodemographic variables considered,

3. by considering sociodemographic characteristics not only of signallers but also of recipients,

4. by considering purely intraspecific communication (only relevant in an evolutionary perspective) as well as tool-use activities (hypothesized to have facilitated the emergence of human language (e.g. Forrester et al. 2013)) when comparing manual laterality between

manipulations and gestures.By tackling these issues during our investigations of non-human primates' manual laterality, the goal of the present PhD thesis was to participate in the research effort made to understand better the evolutionary relationship between the right-handedness and the left-cerebral lateralization of language in humans. In particular, we wondered (1) whether it is possible to evidence effect of social pressures on intraspecific communication considering multiple factors related to social interactions and (2) whether some gesture characteristics are better markers than others of the right-handedness/left-brain specialization for language.

To serve this goal, we had three objectives. The first objective was to provide a detailed insight into the gestural laterality of two of humans' close living relatives, chimpanzees and gorillas, by systematically investigating the production of the most frequent gesture types of their natural specific repertoires. The second objective was to compare our results between these two species. To achieve these first two objectives, we evaluated intraspecific laterality in dyadic interactions of three groups of chimpanzees and three groups of gorillas living under favourable conditions in captivity. For each species, we designed and applied observational and statistical procedures to assess their gestural laterality at the population level as well as to evaluate and to compare the respective influences on gestural laterality of three categories of factors: interactional context components (visual field and body side of both signaller and recipient and emotional valence of context), gesture characteristics (sensory modality, use of communication tool, duration and degree of sharing) and individual sociodemographic characteristics of both signaller and recipient (age, sex, group, hierarchy, kinship and affiliation). The third objective of the present PhD thesis questioned whether manipulation and communication components are controlled by the same left-lateralized cerebral system. To this end, we compared manual laterality in the context of tool use by chimpanzees in non-communication actions and in gestures. First, we compared manual laterality at the population level between non-communication tool use actions similar to termite fishing and each of five frequent conspecific-directed gestures involving a tool; and second, we evaluated whether the expected difference of chimpanzees' manual laterality between non-communication and communication functions (i.e. greater right-hand use for gestures than for manipulation) is modulated by individual sociodemographic characteristics.

In a comparative perspective, we discuss below our main results of our studies with regards to chimpanzees' and gorillas' social structures and dynamics as well as the implications of these results for the evolutionary origins of laterality at the population level and of human language. First, we discuss our findings related to manual laterality at the

population level considering chimpanzees' and gorillas' intraspecific gestures and chimpanzees' tool-use for intraspecific gestures and for manipulations. Second, we discuss the results of our multifactorial investigation of manual laterality for these behaviours. Finally, we conclude and present implications of our results for the evolutionary origins of human cerebral hemispheric lateralization. We then suggest some directions for future research.

1. Manual laterality at the population level

1.1. Chimpanzees' and gorillas' intraspecific gestural laterality

Considering laterality on a continuum, we showed that chimpanzees (resp. gorillas) exhibited a right-hand bias at the population level for the majority (13 of 21) (resp. 9 of 16) of their most frequent intraspecific gestures. From a comparative point of view, it is also interesting to note that 8 of the 14 most frequent gestures performed by both species presented a right-hand bias at the population level (i.e. SLAP HAND, EMBRACE, PUNCH, THROW OBJECT, ATTEMPT TO REACH, PUT OBJECT ON HEAD, SHAKE OBJECT and RAISE ARM).

The direction of asymmetries of most species is generally similar for a majority of individuals in a population (60 to 90% in relation to species and behaviour considered) (e.g. reviews see Bisazza et al. 1998; Vallortigara et al. 1999, 2005; Rogers 2002; Vallortigara & Bisazza 2002). Ghirlanda and colleagues (2009) recently evidenced that unequal numbers of left- and right-lateralized individuals in populations can be explained by an evolutionary stable strategy based on a trade-off between competitive and cooperative intraspecific interactions. Our findings concerning chimpanzees' and gorillas' intraspecific gestural laterality support Ghirlanda and colleagues' (2009) model. Furthermore, we can assume reasonably from our results that the common ancestor of both chimpanzees and gorillas would have had a right-hand preference at least for the 8 above-mentioned gestures. This assumption is supported by other studies of chimpanzees and monkeys that evidence a right-hand bias at the population level:

- for purely intraspecific communication for chimpanzees in captivity (for a category of species-typical gestures combining THREAT, EXTEND ARM and HAND SLAP: Meguerditchian et al. 2010a) and in the wild (for a category of object-manipulation gestures combining OBJECT SHAKE and OBJECT MOVE: Hobaiter & Byrne 2013) as well as for captive olive baboons for HAND SLAP (Meguerditchian & Vauclair 2006),

- for human-directed gestures in captivity by chimpanzees (FOOD BEG: Hopkins & Leavens 1998; Hopkins & Cantero 2003; Taglialatela et al. 2006; FOOD BEG and POINTING (pooled data): Hopkins et al. 2005a; THROW OBJECT: Hopkins et al. 1993; CLAPPING: Meguerditchian et al. 2012; a category of species-typical gestures including THREAT, EXTEND ARM and HAND SLAP: Meguerditchian et al. 2010a), by olive baboons (FOOD BEG: Meguerditchian & Vauclair 2009; POINTING: Meunier et al. 2012; HAND SLAP: Meguerditchian & Vauclair 2006; Meguerditchian et al. 2011), and for POINTING by red-capped mangabeys and Campbell's monkeys (Maille et al. 2013a) as well as Tonkean macaques (Meunier et al. 2013b),
- for THROW OBJECT directed towards both humans and conspecifics (pooled data) by chimpanzees (Hopkins et al. 2005b).

By evidencing a population-level right-hand bias for the majority of chimpanzees' and gorillas' most frequent intraspecific gestures performed in various social contexts, our findings as well as those of the three studies mentioned above (chimpanzees: Meguerditchian et al. 2010a; Hobaiter & Byrne 2013; baboons: Meguerditchian & Vauclair 2006) showed that such bias is present in purely intraspecific communication and not limited to interspecific communication. More generally, our findings support a growing literature evidencing a predominance of right-hand use in gestural communication by some non-human primates and suggesting that gestural laterality would be a prerequisite of the language left-specialization.

Chimpanzees (resp. gorillas) did not exhibit a right-hand bias for 8 of the 21 (resp. 7 of the 16) other gestures considered. We did not evidence a significant right-hand bias at the population level for four of the 14 frequent gestures performed by both species (i.e. EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, and TOUCH BODY) (however, we found a trend towards the right side at the population level for EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL for gorillas). Absence of a significant population level hand preference for tactile gestures was also evidenced by two other studies investigating laterality in purely intraspecific communication for TOUCH OTHER and EMBRACE for chimpanzees (Fletcher & Weghorst 2005) and for TOUCH BODY, TOUCH GENITAL, EMBRACE LATERAL and MOVING WITH ARMS AROUND THE PARTNER for bonobos (same gestures as EMBRACE HALF but labelled differently) (Chapelain 2010). These findings suggest that sensory modality could modulate chimpanzees' and gorillas' intraspecific gestural laterality, an effect which was evidenced by our multifactorial investigation.

1.2. Chimpanzees' manual laterality for tool use in non-communication actions and intraspecific gestures.

Our study compared chimpanzees' manual laterality in non-communication actions similar to termite fishing and in intraspecific gestures involving a communication tool. Considering laterality on a continuum, we evidenced a right-hand use bias at the population level for each of the five conspecific-directed gestures involving a tool, but not for the non-communication tool-use actions.

Our results for the non-communication tool use actions agree with Hopkins and colleagues' (2009) report that did not show any evidence of a population-level bias for captive chimpanzees' tool-use task designed to simulate termite fishing. However, our results do not agree with those studies of wild chimpanzees for termite fishing (Bogart et al. 2012; Lonsdorf & Hopkins 2005; McGrew & Marchant 1992, 1996, 1999) showing a population-level left-hand bias. We hypothesized that differences between these studies and ours could be attributed in part to 1) effects of genetic factors and/or social learning on laterality as suggested by Lonsdorf and Hopkins (2005) to explain task-specific variations of the direction of laterality between groups of wild chimpanzees for tool-use and, 2) to differences of haptic and sensory requirements during insertion and extraction (Hopkins et al. 2009) between our non-communication tool use actions and termite fishing in the wild. Indeed, Hopkins and colleagues (2009) pointed out: "termite fishing has large sensory and haptic components, since the chimpanzees must feel when the stick has accumulated a sufficient number of termites before extracting it from the mound and then take care not to lose termites by bumping the stick during extraction" p. 9. The non-communication tool use actions considered did not require that particular type of haptic discrimination.

We evidenced a population-level right-hand bias for each of the five intraspecific gestures involving a communication tool. These findings agree with previous studies of manual laterality of object-manipulation gestures directed towards conspecifics by wild chimpanzees (Hobaiter & Byrne 2013), and directed towards humans (Hopkins et al. 1993) and towards both humans and conspecifics (pooled data) (Hopkins et al. 2005b) by captive chimpanzees. Therefore, all these findings concerning chimpanzees' gestures involving a communication tool further favour the origin of human language theory (e.g. Corballis 2002, 2003) proposing that gestural laterality would be a precursor of language specialization of the left brain.

We discuss below mechanisms/factors underlying manual laterality of gestures and manipulation in the light of our multifactorial analysis.

2. Multifactorial investigation of manual laterality

Considering several categories of gestures instead of limiting our investigation to the microlevel of distinct gestures allowed us to explore gestural laterality in depth. To further our investigation, we took into account simultaneously multiple additional factors expected to influence gestural laterality. We evidenced that chimpanzees' and gorillas' intraspecific gestural laterality was influenced by several factors and their mutual intertwinement: interactional context (visual fields of both signaller and recipient as well as emotional context), gesture characteristics (sensory modality, use of a communication tool, sharing degree, and gesture duration) and by certain socio-demographic components, in particular signaller's hierarchical rank, and to a lesser extent signaller's age. These analyses revealed similarities but also differences between the two species. More precisely, chimpanzee signallers used their hand ipsilateral to the recipient for tactile and visual gestures, and their contralateral hand for gestures involving the auditory sensory modality and a communication tool. Right-hand use by chimpanzee signallers' was more important in negative contexts for common gestures and by subordinate signallers for tactile gestures. Gorilla signallers used their hand ipsilateral to the recipient for tactile and visual gestures whatever the emotional context, gesture duration, sex of recipient or kin relationship between signaller and recipient, and whether a communication tool was used or not. Signallers' contralateral hand was never used preferentially in any situation. Gorilla signallers' right-hand use was particularly pronounced in negative contexts, for short gestures as well as by female signallers and increased with age.

We discuss our results in a comparative approach between chimpanzees and gorillas, considering, first, the factors we found without effect on both gorillas' and chimpanzees' gestural laterality, then our findings concerning lateralization of emotional processing of gestures as well as modulation of gestural communication lateralization by communication strategies and by social selection pressures. Considering chimpanzees' manual laterality in the context of tool use in intraspecific gestural communication and manipulation, we then focus on the effects of age, sex and hierarchy, allowing us to address the effects of the function *per se*. Finally, we comment our findings in relation to theories concerning the evolutionary

origins of human cerebral hemispheric lateralization and then suggest important issues for future research.

2.1. Factors without effect on both chimpanzees' and gorillas' gestural laterality

Our results concerning chimpanzees and gorillas did not evidence any significant influence of kinship, recipients' sex and hierarchy on signallers' right-hand use. It is interesting to note that these ineffective factors concern only recipients' characteristics. Contrary to our expectations, our findings overall suggest that these recipients' characteristics did not play a role in determining chimpanzees' and gorillas' gestural laterality.

2.2. Lateralization of emotional processing of gestures

Our findings suggested that signallers' emotional state (emotional valence *per se* and stress-related emotional states) would affect their gestural laterality through the emotional valence associated with the social interaction (positive vs. negative), signallers' hierarchical status as well as perception of recipients' facial expressions of emotions (more pronounced on their left hemiface than on their right hemiface).

Considering emotional valence, we found that gorilla signallers' right-hand use was particularly pronounced in negative contexts and this was also true for chimpanzee signallers performing common gestures. These findings agree with Rohlfs and Ramirez's (2006) review stressing the importance of distinguishing emotional valence (positive-negative) and motivational direction (approach-withdrawal) and showing that "anger" (negative in valence, (e.g. Lazarus 1991) and which frequently elicits approach motivation (e.g. Berkowitz 1999) enhanced activity in humans' left-prefrontal brain leading to right-hand preference in negative emotional contexts (e.g. Harmon-Jones 2004).

Considering signallers' hierarchical status, subordinate chimpanzees and gorillas were overall more right-handed than intermediate subjects. Moreover, subordinate chimpanzees were overall right-handed than dominants. These differences may be the consequence of higher levels of psychosocial stress (e.g. competition for access to food and space) experienced by subordinates leading to a greater right-hand use; it must be noted that captivity could exacerbate psychosocial stress (Muller & Wrangham 2004). Indeed, stress would elicit a right-side bias at the population level (rats: e.g. Alonso et al. 1991; Castellano et al. 1987, 1989; anoles: Deckel 1998) possibly because it would inhibit the right hemisphere. This assumption is supported by the Rohlfs and Ramirez's (2006) review of reports concerning

humans mentioning that stress could induce several neurochemical changes (e.g. increase of dopamine: Bertollucci-D'Angio et al. 1990) causing structural and functional alterations in the right hemisphere (Joseph 1994; Schore 1997; Ben-Shachar et al. 1994). Contrary to our results for chimpanzees, subordinate gorillas were not more right-handed than dominants. This difference could be due to the social structure[23] of gorillas who live in polygamous harem groups. Competition for reproduction would probably induce a certain amount of stress among high-ranking gorillas (mostly females): psychosocial stress caused by the reproduction strategy adopted by high-ranking females, particularly La Vallée females (personal observations), would increase right-hand use as previously hypothesized.

Considering the perception of recipients' facial expressions of emotions, our results showed that chimpanzee and gorilla signallers were overall right-handed more when they were in recipients' left visual field during an interaction (RVF_L) than in recipients' right visual field (RVF_R). We assumed that recipients' more pronounced facial expressions of emotions on the left than on the right hemiface (e.g. chimpanzees: Wallez et al. 2012; rhesus macaques: Hauser 1993; baboons: Wallez & Vauclair 2011; humans: Nicholls et al. 2002) could enhance signallers' emotional state during an interaction and would thus explain signallers' greater right-hand use in RVF_L. Indeed, as previously detailed, emotion and stress are thought to modulate use of right hand.

2.3. Lateralization of gestures: modulation by communication strategies

Our findings suggested that both chimpanzees' and gorillas' use of communication strategies depended on gesture characteristics (i.e. tactile, visual or auditory gestures; gestures involving or not the use of a communication tool).

Considering gesture sensory modality, chimpanzees and gorillas used their right hand to perform tactile gestures (implying physical contact with recipient) and visual gestures (implying transmission of a visual signal) more when the recipient was in their right visual field during an interaction (SVF_R) than in their left visual field (SVF_L). We hypothesized that they used the hand ipsilateral to the recipient to facilitate transmission of these signals. Conversely to tactile and visual gestures, chimpanzee signallers used preferentially their hand on the side opposite to the recipient (i.e. contralateral hand) for auditory gestures. Our observations enabled us to hypothesize that when they plan to perform an auditory gesture,

[23] According to the definition of Kappeler and Van Schaik (2001), "social structure refers to the pattern of social interactions and the resulting relationships among the members of a society" p. 710.

they kept their hand close to the recipient free to be used for further potential tactile or visual gestures towards the recipient (e.g. for a PUSH).

Considering gestures involving the use of a communication tool, chimpanzee and gorilla signallers used their right hand more for gestures with an object than for gestures without an object when the recipient was in their left visual field (SVF_L) and conversely in SVF_R situation. In other words, they used preferentially more their hand contralateral to the recipient to communicate with an object. Personal observations suggested that they did so possibly to prevent the recipient from grabbing the potentially coveted object used as a communication tool and/or to keep their hand ipsilateral to the recipient free to be used for a potential additional gesture towards the latter.

Experimental studies investigated non-human primates' communication strategies (great apes: Hostetter et al. 2001; Liebal et al. 2004b, 2004c; monkeys: Maille et al. 2012; Bourjade et al. 2014). For example, Liebal and colleagues' (2004b) showed that when chimpanzee signallers interacted with an inattentive recipient, they tended either to approach it frontally before starting to interact or moved around the inattentive recipient to position itself in the recipient's attentional field before performing a visual gesture. These authors suggested that chimpanzee signallers do not seem to use attention-getting behaviours (e.g. auditory gestures) to manipulate recipients' attentional state, but used strategies based on moving towards the recipient to make sure that the latter is attentive before performing a visual gesture.

2.4. Lateralization of gestures: modulation by selection pressures in relation to social structure and dynamics

In accordance with the social theory of the origins of laterality (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009), authors suggested that asymmetry at the population level should be particularly present in social species whereas non-social species would more likely to be lateralized only at the individual level (bees: Anfora et al. 2010; fish: Bisazza et al. 2000; humans: Abrams & Panaggio 2012). These findings suggested that alignment of laterality at the population level may result from social pressures. The influence of social pressures on humans' manual laterality (e.g. forced right-hand use for writing and eating; positive reinforcement) has been evidenced (e.g. see reviews Llaurens et al. 2009; Schaasfma et al. 2009).

Our between-species comparisons suggest that social selection pressures might have acted on the gestural laterality of our close living relatives that are chimpanzees and gorillas. Indeed, we hypothesized that the social structure and dynamics of these species impacted differently the influence of the following factors on gestural laterality: gesture sensory modality, degree of gesture sharing, as well as signallers' hierarchical rank, sex, age and group.

Considering gesture sensory modality, chimpanzee signallers overall used their right hand for visual more than for tactile and auditory gestures and more for tactile than for auditory gestures. On the contrary, gorilla signallers overall used their right hand more for auditory than for visual and tactile gestures. Pika and colleagues' (2005b) review showed that visual and tactile gestures were more common than auditory gestures in chimpanzees' and gorillas' gestural repertoires. These authors also noted that auditory gestures represented a greater part (about one fifth) of gorillas' than of chimpanzees' (about one-tenth) gestural repertoire. We hypothesize that this difference may be due to the generally higher interindividual distances kept by gorillas (Klein 1999) compared to chimpanzees (Harcourt 1979); these distances would make auditory signals particularly relevant for gorillas to attract more easily the attention of an audience. As auditory gestures are more common in gorillas' repertoire, they would be more codified/lateralized than for chimpanzees, possibly for better social coordination.

We evidenced that the degree of gesture sharing effected only chimpanzee signallers' right-hand use. Chimpanzee signallers used their right hand overall more for common gestures than for rare gestures, possibly because common gestures benefit by being more codified/lateralized than rare gestures, resulting in potentially more coordination that facilitates interactions and thus social cohesion. We suppose that this facilitation of cohesion would especially benefit chimpanzees living in groups characterized by a higher variable group membership compared to gorillas that generally live in cohesive groups (Aureli et al. 2008). It must be noted that chimpanzee signallers tended to be right-handed more for gestures towards females than towards males. This could be explained by the fact that most chimpanzee signallers interacting with females were males using common gestures. We assume that facilitation of social interactions provided by the use of common gestures would be particularly beneficial in terms of fitness (e.g. reproduction success) concerning males' gestures directed towards females for chimpanzees living in multi-male/multi-female groups (e.g. Goodall 1968) where dominant and subordinate males have access to females (e.g. Wroblewski et al. 2009) but not for western lowland gorillas living in polygamous harem

groups controlled by a sexually mature silverback male (e.g. Gatti et al. 2004) and characterized by a one-male mating system as subordinate males generally leave their natal group to become solitary before reaching full sexual maturity (e.g. Robbins et al. 2004)

Considering signallers' hierarchical rank, as previously hypothesized (see above discussion of lateralization of emotional processing of gestures), differences of laterality patterns between gorillas and chimpanzees may be the consequence of the reproduction competition strategy particular to high-ranking female gorillas.

Considering signallers' sex, female gorilla signallers were overall more right-handed than male signallers. Differently, our findings did not evidence any effect of chimpanzee signallers' sex on their use of right hand. In the light of gorillas' particular social structure we suppose that competition for reproduction between females would induce a certain amount of psychosocial stress (particularly among high-ranking gorillas who were mostly females) that would increase right-hand use (see above discussion of laterality of emotional processing). Further investigations are required to understand better the influence of sex on primates' gestural laterality and its determinants.

Considering signallers' age, our results indicated that infant gorilla signallers were significantly right-handed more for gestures towards mature adult recipients than towards young adult recipients. However, we did not evidence any effect of chimpanzee recipients' age class on signallers' right-hand use. This difference between the two species could be explained by the above-mentioned effect of psychosocial stress experienced by infant gorilla signallers interacting with fully mature individuals. In fact, harassment of mothers and especially of their infant(s) by other females appeared more aggressive in our gorilla groups (particularly at Burgers' zoo) than in the chimpanzee groups (personal observation). This reproduction competition would be exacerbated for gorillas because of their particular social structure.

Considering signallers' group, we evidenced overall a group effect on gorilla signallers' right-hand use. These differences between groups/zoos may be the consequence of social pressures suggested to explain laterality differences between social groups in communication activities (Ghirlanda and Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009). However, we did not evidence any clear differences between chimpanzee groups/zoos: differences in signallers' right-hand use were found between two groups only for auditory gestures. We hypothesized that gorillas' social structure organized around a single individual would be more likely to elicit differences in gestural laterality between groups than chimpanzees' social structure of small subgroups controlled by

a high degree of fission-fusion dynamics. To this hypothesized distal cause, we could add a proximal cause related to adults' male-female ratios that differed more between gorilla groups (La Vallée: 0.33; Apenheul: 0.25; Burgers': 0.5) than between chimpanzee groups (Leipzig, Beauval, La Palmyre: 0.25). Further comparisons between other groups of gorillas and chimpanzees as well as between other species living in harems and multi-male/multi-female groups are necessary to confirm these hypotheses.

2.5. Manual lateralization of gestures and manipulation: modulation by sociodemographic factors

Considering both communication and non-communication functions, our multifactorial studies evidenced an age effect on manual laterality. Our findings overall support previous studies (e.g. see review by McGrew & Marchant 1997) showing that direction of hand preference becomes more salient with age, proposing that hand preference could be due to maturation and/or the result of practice, learning and experience. However, we evidenced a decrease of right-hand use by elder chimpanzees possibly due to physical limitations, lower activity (documented for humans: Hughes et al. 1997; Schut 1998; Ranganathan et al. 2001) and/or lower sociality associated with aging that could decrease practice-based performance of the right hand that would thus converge towards the performance of the left hand. To our knowledge, this is the first evidence of a possible senescence effect on manual laterality of non-human primates. The influence of signallers' sex on hand use for gestures and manipulation, however, remains unclear and further research is required to document the influence of sex on manual laterality and its determinants.

The interpretation of the effect of signallers' hierarchical rank on chimpanzees' manual laterality for tool-use for both communication and non-communication functions suggested an effect of psychosocial stress in manipulation hypothesized to increase right-hand use. Our findings concerning dominant chimpanzees (potentially free from psychosocial stress and haptic constraints for tool-use to obtain food) showing that they were more right-handed for gestures than for manipulations support the hypothesis that some non-human primates and young children have a specific left-hemisphere processing of gestural communication distinct from the cerebral system involved in non-communication manual actions (e.g. Meguerditchian & Vauclair 2009).

3. General conclusion and directions of future research

To conclude, the present PhD thesis provides significant contributions concerning implications for the evolutionary origins of laterality at the population level and of human language. Indeed, this work investigating non-human primates' manual laterality addressed several issues concerning laterality.

Our study convincingly showed that our chimpanzee and gorilla subjects were right-handed at the population level for the majority of the most frequent gesture types of their respective natural communication repertoires (of which 8 frequent gestures are common to both species). To our knowledge, this is the first evidence of a population-level right-hand bias for gorillas' purely intraspecific gestures.

Our multifactorial approach showed for the first time in primates that laterality in gestural communication and in manipulation is modulated by several factors and their interactions. Considering purely intraspecific gestural communication, laterality of chimpanzees' and gorillas' most frequently expressed gestures was particularly modulated by characteristics associated with interactional context (visual fields of both signallers and recipients as well as emotional contexts), gesture characteristics (sensory modality, use of a communication tool and sharing degree) and by socio-demographic components, especially signallers' hierarchical rank and, to a lesser extent, signallers' age. Our findings revealed similarities and dissimilarities between the two species that may be related 1) to the lateralization of emotional processing (emotional valence *per se* and stress-related emotional state of signallers), 2) to the lateralization of gestures with possible use of different communication strategies depending on the type of gestures performed by chimpanzees and gorillas, and 3) to the lateralization of gestures stemming from social selection pressures related to the social structure and dynamics of the studied species. Considering now both communication and non-communication functions, our multifactorial analyses showed the influence of individual sociodemographic characteristics on manual laterality with the first evidence of an effect of hierarchical rank and of a possible senescence effect on the manual laterality of non-human primates. Nevertheless, our results concerning the influence of signallers' sex on intraspecific gestures and on manipulation are less clear and additional investigations are necessary to understand better the effects of sex on manual laterality and their determinants.

As a conclusion, our findings concerning chimpanzees lead us to hypothesize that right-side predominance in primates for gestures without a tool (involving only

communication components) is greater than for gestures with a tool (involving both communication and manipulation components) that is in turn greater than for non-communication actions with a tool. Although non-communication actions with a tool elicited strong laterality (direction and particularly strength), we did not evidence a related population-level right-hand bias. Therefore, our overall results support partly the "tool-use hypothesis" (e.g. Greenfield 1991; Higuchi et al. 2009; Forrester et al. 2013) in the sense that complex temporal sequences with high sensorimotor requirements of tool-use for both communication and non-communication activities induce a strong right-hand use. However, it would be necessary to test these three hypotheses on other spontaneous tool use actions such as wadge-dipping (Boesch 1991). Further studies are thus necessary to confirm whether tool-use could have been an essential selection pressure determining the emergence of the two most pronounced manifestations of humans' hemispheric specialization that are right-handedness for manipulation and left-hemispheric specialization for language. Finally, our studies of chimpanzees' and gorillas' intraspecific gestural laterality overall support Ghirlanda and colleagues' (2009) model postulating that population-level biases can be explained by an evolutionary stable strategy based on intraspecific interactions. Moreover, our results support the origin of human language theory (e.g. Corballis 2002, 2003) stating that gestural laterality represents a prerequisite of the language left-brain specialization. In addition, our findings concerning chimpanzees' manual laterality for tool use in intraspecific gestures and manipulation provide additional support to the hypothesis that some primate species may have a specific left-hemisphere processing of gestural communication distinct from that processing non-communication manual actions (e.g. Meguerditchian & Vauclair 2009).

To further our understanding of the evolutionary origins of laterality at the population level and of human language, our findings emphasize the importance for further studies:

1) to consider socioecologically relevant contexts, namely contexts in which subjects interact with conspecifics in environments ensuring subjects to behave as naturally as possible: in the wild and/or in favourable captivity conditions (when naturalization of enclosures is stimulating and social groups include many subjects);

2) to investigate the intraspecific gestural laterality (only relevant in an evolutionary perspective) of humans and other closely-related living species (i.e. great apes: bonobos and orang-utans), and lesser apes and monkeys with various social structures, dynamics and degrees of sociality;

3) to apply relevant data collection and analyses: large sample size and numerous data points per subject, independence of data, multiple potentially influential factors considered and powerful statistical analysis assessing the respective influence of these factors and their interactions.

Using these methodologies will also help us understand better the causes of differences between both studies and species.

CHAPTER 6

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French summary of the PhD manuscript

I - Introduction

1. Latéralisation cérébrale : un phénomène répandu

Considérée longtemps comme spécifique aux humains, la latéralisation du cerveau et du comportement au niveau d'une population a été démontrée dans toutes les classes de vertébrés (e.g. Rogers et al. 2013) et plusieurs phylums des invertébrés (e.g. Frasnelli 2013). L'ubiquité apparente du phénomène de latéralisation du cerveau dans le règne animal suggère que du point de vue de l'évolution, elle contribue de manière significative à la fitness.

Selon la théorie de l'évolution de la latéralité au niveau populationnel (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009), la latéralisation du cerveau a pu avoir évolué selon deux étapes. D'abord, des biais au niveau individuel auraient été sélectionnés car ils améliorent les capacités cognitives en évitant la réplication des fonctions et la concurrence hémisphérique (e.g. Corballis 1989) et en permettant le traitement simultané de différentes sources d'information (e.g. Rogers 2002). En second lieu, les biais au niveau des populations pourraient avoir été sélectionnés au terme d'une Stratégie Evolutionnaire Stable (Evolutionarily Stable Strategy, ESS) basée sur des interactions proie-prédateur interspécifiques. Ces biais auraient apporté des avantages grâce à la coordination de comportements d'organismes asymétriques mais également des désavantages en rendant les comportements des proies plus prévisibles par les prédateurs (e.g. bancs de poissons: Vallortigara & Bisazza 2002). Ghirlanda et collègues (2009) ont proposé cependant que la latéralité au niveau populationnel pourrait être expliquée par une ESS basée sur un compromis entre des interactions intraspécifiques concurrentielles et coopératives plutôt que par des interactions interspécifiques. La latéralité sociale serait ainsi apparue au niveau populationnel parce qu'elle faciliterait les interactions intraspécifiques (Rogers 2000) comme démontré chez les invertébrés (e.g. Frasnelli et al. 2012b) et les vertébrés (e.g. Baraud et al. 2009). Ces résultats montrent l'importance d'étudier la latéralité non seulement dans des interactions interspécifiques mais également intraspécifiques.

Afin de mieux comprendre l'origine évolutive de la préférence manuelle à droite au niveau populationnel et de la latéralisation cérébrale à gauche pour le langage chez l'humain, étudier le modèle primate et en particulier les grands singes peut fournir des indices précieux (e.g. Corballis 2002; Meguerditchian et al. 2013).

2. Pertinence des primates non-humains comme modèle pour l'étude de l'origine du langage

Les primates non-humains sont les espèces phylogénétiquement les plus proches des humains (e.g. Langergraber et al. 2012). De plus, ils montrent une ressemblance remarquable avec les humains en termes d'anatomie de la main (e.g. Aiello & Dean 1990) et de capacité de manipulation (e.g. Byrne et al.2001) aussi bien qu'en terme d'asymétrie cérébrale neuroanatomique (e.g. Cantalupo & Hopkins 2001). Les primates sont également des modèles appropriés pour étudier les origines du langage. La latéralité gestuelle des primates et en particulier de nos plus proches parents vivants, les grands singes, est l'objet d'un nombre toujours croissant d'études (e.g. Shafer 1987; McGrew & Marchant 1997; Hopkins et al. 2012; Meguerditchian et al. 2013). Ces études ont alimenté les récents débats scientifiques sur les origines du langage en fournissant des arguments en faveur de son origine gestuelle (Arbib et al. 2008; Corballis 2002; McNeill 2012). Un premier argument en faveur de la théorie de l'origine gestuelle du langage est que la communication gestuelle des primates est plus flexible en termes d'apprentissage et d'usage, que leur vocalisations (e.g. Call & Tomasello 2007; Meguerditchian & Vauclair 2008). En effet, elle est très flexible, selon le contexte social, le rang social et l'âge des individus, ce qui a pour conséquence de produire d'importantes variations entre les individus et entre les groupes d'une même espèce, et ce, au niveau de la composition, la morphologie et la taille du répertoire (e.g. Maestripieri 1999; Call & Tomasello 2007; Pika et al. 2005a; Pika 2008a; Arbib et al. 2008; Hobaiter & Byrne 2011). Au contraire, en ce qui concerne le répertoire vocal, la variation est moindre au niveau de sa composition et de sa taille, entre les individus et entre les groupes d'une même espèce (e.g. Meguerditchian & Vauclair 2014). Un deuxième argument est fourni par la découverte récente, chez les humains et chez des espèces de singes, des neurones miroirs que l'on suppose présents dans les cerveaux de tous les primates (e.g. Fabbri-Destro & Rizzolatti 2008). Ces neurones, impliqués dans la production et la perception des actions visuo-gestuelles et de communication oro-faciale, sont situés dans la région cérébrale F5, homologue au secteur de production du langage chez l'humain (e.g. Nishitani & Hari 2000). En outre, l'étude de la spécialisation hémisphérique pour la communication montre une prédominance, dans l'hémisphère cérébral gauche, chez l'homme, de l'aire de Broca (responsable de la production du langage) et de l'aire de Wernicke (responsable de la compréhension de la parole) (Horwitz et al. 2003; Xu et al. 2009) ainsi que chez les grands

singes des secteurs homologues (e.g. Gannon et al. 1998). Corrélativement, les observations des grands singes en captivité ont montré que leurs gestes[24] étaient exprimés principalement par la main droite (e.g. McGrew & Marchant 1997). Un troisième argument est l'inter-relation profonde entre langage humain et latéralité des gestes avec une utilisation prédominante de la main droite pour (i) les gestes accompagnant la parole (e.g. Kimura 1973a), (ii) la langue des signes par les malentendants (e.g. Bellugi 1991) et (iii) les gestes précédant la parole chez les jeunes enfants (e.g. Blake 2000). Un quatrième argument en faveur de l'origine gestuelle du langage est que le système de communication gestuelle des primates partage plusieurs caractéristiques essentielles avec le langage humain comme l'intentionalité (e.g. Call & Tomasello 2007; Meguerditchian & Vauclair 2006) et des propriétés référentielles (e.g. imperative POINTING[25]: Leavens & Hopkins 1999; DIRECTED SCRATCHING: Pika & Mitani 2006; BECKONING: Genty & Zuberbühler 2014). Toutes ces propriétés, nécessaires à la production et à l'utilisation d'une communication gestuelle élaborée sont des conditions indispensables au langage humain). Les primates non humains et particulièrement les grands singes s'avèrent être ainsi de bons modèles pour explorer la phylogénie de la latéralisation hémisphérique liée à la communication gestuelle, dans la perspective d'une possible contribution des gestes à l'émergence du langage humain au cours de l'évolution.

3. Préférence manuelle chez les primates non-humains

3.1. Communication gestuelle

De nombreuses d'études en captivité et en milieu naturel ont montré un système de communication gestuelle complexe et flexible chez les primates non-humains et particulièrement les grands singes (e.g. Call & Tomasello 2007). Premièrement, la taille de leur répertoire gestuel est considérable et montre une grande variété de gestes (e.g. Call & Tomasello 2007; Pollick & de Waal 2007). Deuxièmement, certaines espèces de primates non-humains peuvent produire des gestes intentionnels. Ceci signifie que ces gestes exécutés par un émetteur doivent servir à atteindre un but social et sont orientés vers un destinataire particulier comme indiqué par l'orientation du corps, l'alternance du regard et/ou un contact physique avec le receveur. Cela signifie aussi qu'ils sont destinés à produire une réponse du receveur comme indiqué par le regard en direction de celui-ci, et/ou la persistance communicative au cas où il ne réagirait pas ou lorsque la réponse du destinataire n'a pas

[24] Dans cette présente thèse de doctorat, le terme "geste" est restreint à la fonction de communication (Pika & Bugnyar 2011).
[25] Dorénavant, les gestes sont écrits en petites majuscules

correspondu à l'attente de l'émetteur (e.g. Call & Tomasello 2007; Pollick & de Waal 2007). Troisièmement, les gestes des primates non-humains sont également caractérisés par une flexibilité d'utilisation (e.g. Call & Tomasello 2007). Quatrièmement, il a été montré que les primates non-humains, et en particulier tous les grands singes, ajustent leur communication gestuelle à l'état d'attention du receveur: par exemple, l'émetteur fait plus de gestes vers un individu orienté dans sa direction et/ou utilise un type approprié de geste (e.g. Call & Tomasello 2007). A partir de nombreuses études ayant traité de la latéralité manuelle chez les primates non-humains ont émergé plusieurs hypothèses concernant l'origine de la préférence manuelle humaine ainsi que plusieurs points importants de méthodologie.

3.2. Latéralité manuelle chez les primates non-humains: hypothèses sur les origines de la préférence manuelle chez l'humain et questions méthodologiques.

3.2.1. Hypothèses concernant l'origine de la préférence manuelle chez l'humain

Quatre hypothèses principales ont été émises pour expliquer les origines de la préférence manuelle chez l'humain.

1) L'hypothèse de l'origine posturale (MacNeilage et al. 1987) stipule que la latéralité manuelle des primates serait issue d'adaptations structurelles et fonctionnelles pour la recherche de nourriture. Celle-ci serait apparue en deux étapes. Tout d'abord, la préférence pour la main gauche serait apparue à l'occasion d'actions unimanuelles visuellement guidées de prédation (telle que manipulation de fruit) tandis que la main droite aurait été utilisée pour la stabilité de la posture et de la locomotion arboricole. Dans un deuxième temps, l'évolution des primates vers la locomotion terrestre a pu avoir permis à ceux-ci de se libérer de la restriction posturale liée au mode de vie arboricole et par conséquent à leur main droite de se spécialiser pour des tâches avec certain niveau d'exigence haptique telle que la manipulation bimanuelle. L'hypothèse de l'origine posturale suggère que la complexité de la tâche conduirait à utiliser la main droite seulement pour un certain niveau de la demande haptique, ce qui est en conformité avec les hypothèses suivantes.

2) L'hypothèse artéfactuelle considère que la préférence manuelle des primates serait une conséquence de facteurs expérimentaux (Warren 1980) et/ou environnementaux liés à la captivité (e.g. McGrew & Marchant 1997). Selon Warren (1980), l'apprentissage induit par la pratique (d'un dispositif expérimental par exemple) aboutirait à une préférence manuelle plus marquée que pour des actions quotidiennes spontanées (e.g. geste simple pour prendre de la nourriture au sol).

3) L'hypothèse de la complexité de la tâche proposée par Fagot et Vauclair (1991) prévoit une absence de latéralité (un modèle ambidextre) dans les tâches de manipulation de faible niveau de complexité (i.e. comportant une action unique tel que l'atteinte d'un item) et une préférence manuelle plus marquée dans les tâches comportant un niveau élevé de complexité. Il a été ainsi proposé que la latéralité dans des tâches complexes exigeant de la précision telles que l'utilisation d'outil auraient contribué à l'apparition d'une latéralisation hémisphérique gauche pour les fonctions motrices et le langage chez l'humain (e.g. Frost 1980; Forrester et al. 2013). Ceci a conduit plusieurs chercheurs à émettre l'hypothèse que l'utilisation d'outil en tant que tel aurait ainsi joué un rôle essentiel dans l'émergence de la préférence manuelle humaine pour la main droite.

4) L'hypothèse de l'utilisation d'outil postule que la prédominance de l'utilisation de la main droite chez l'humain est liée à l'utilisation d'outil et était déjà présente chez l'ancêtre commun aux humains et aux grands singes (e.g. Greenfield 1991). Cette hypothèse est confortée par des études ayant montré que les actions utilisant la main droite sont associées à la capacité de l'hémisphère cérébral gauche de traiter des séquences temporelles complexes d'activités motrices comme celles exigées pour la fabrication et l'utilisation d'outil (e.g. Foucart et al. 2005). L'aptitude au langage serait ainsi née d'une extension de cette capacité de l'hémisphère cérébral gauche.

A travers ces hypothèses, nous pouvons voir que la posture, la complexité de la tâche et l'utilisation d'outil ont vraisemblablement influencé l'évolution de l'asymétrie manuelle chez les primates. Il faut noter cependant qu'il a été montré que des facteurs complémentaires modulent la latéralité manuelle et doivent par conséquent être considérés à la fois pour éviter des résultats et/ou interprétations erronés ainsi que des inconsistances entre études.

3.2.2. Facteurs modulant la latéralité manuelle

Plusieurs facteurs complémentaires moduleraient la latéralité manuelle dans les actions non-communicatives et les gestes, en direction, force et/ou consistance (chez et entre les sujets ainsi que dans et entre les tâches) chez des espèces de primates dont les singes de l'Ancien et du Nouveau Monde ainsi que les grands singes (e.g. McGrew & Marchant 1997; Meguerditchian et al. 2013). Parmi ces facteurs, nous pouvons mentionner 1) les différentes caractéristiques sociodémographiques âge (e.g. Boesch 1991), sexe (e.g. Sommer & Kahn 2009) et parenté (e.g. Hopkins 1999), 2) les caractéristiques liées au contexte (position du receveur: Meunier et al. 2011) et 3) le type de geste (e.g. Hobaiter & Byrne 2013). Jusqu'à

présent, seulement quelques types de gestes ont été considérés. À notre connaissance, aucune étude n'a abordé l'effet possible sur la latéralité manuelle du rang hiérarchique, du contexte émotionnel, de la modalité sensorielle des gestes (tactile, visuel, auditif), du degré de partage des gestes (gestes communs exécutés par la plupart des sujets d'une population ou gestes rares exécutés par seulement quelques sujets) et de la durée du geste (long ou bref). Il est donc essentiel d'aller plus loin en considérant le plus grand nombre possible de ces facteurs dans l'étude de la latéralité manuelle. En outre, il est particulièrement important de prendre en compte les questions de méthodologie qui peuvent également être sources de biais menant à des résultats et/ou des interprétations incorrects ainsi qu'à d'apparentes contradictions entre études.

3.2.3. Questions méthodologiques

La littérature sur la préférence manuelle chez les primates met en évidence plusieurs questions méthodologiques aussi bien que des inconsistances entre études qui rendent les comparaisons difficiles comme la terminologie, la méthode de mesure (actions spontanées ou tâches expérimentales, actions non-communicatives ou gestes, gestes dirigés vers des humains et/ou des conspécifiques), les conditions de vie (captivité ou milieu naturel) ainsi que les procédures liées au recueil et à l'analyse des données. Une autre source de disparités entre études est l'absence d'approche globale prenant en considération simultanément les multiples facteurs pouvant influencer la latéralité gestuelle ainsi que leurs interactions. Une telle approche avec une procédure statistique utilisant des Modèles Linéaires Généralisés Mixtes est mise en œuvre dans la présente thèse.

4. Originalité et objectifs de l'étude

Etudier la latéralité gestuelle dans des conditions socio-écologiques proches des conditions où la sélection naturelle a opéré est particulièrement important du point de vue de l'évolution. Ainsi, l'étude doit considérer des contextes où les sujets interagissent avec des conspécifiques dans des environnements tels que le milieu naturel et/ou captivité en conditions favorables (avec naturalisation optimale des enclos et groupes sociaux composés d'un nombre important de sujets). Seulement peu d'études ont étudié la latéralité gestuelle des primates dans la communication purement intraspécifique (chimpanzés: Fletcher & Weghorst 2005; Meguerditchian et al. 2010a; Hobaiter & Byrne 2013; bonobos: Chapelain 2010; babouins olives: Meguerditchian & Vauclair 2006). De plus, peu d'études ont comparé la

latéralité manuelle dans la manipulation et dans la communication gestuelle (chimpanzés: Hopkins et al. 2005a; Meguerditchian et al. 2010a ; mangabeys à collier et singes de Campbell: Maille et al. 2013; macaques de Tonkean: Meunier et al. 2013b; babouins olives: Meguerditchian & Vauclair 2006, Meguerditchian et al. 2011; Meguerditchian & Vauclair 2009; Meunier et al. 2012; jeunes enfants: Bates et al. 1986; Bonvillian et al. 1997; Vauclair & Imbault 2009; Cochet et al. 2011; Esseily et al. 2011; Meunier et al. 2012). Les comparaisons réalisées par ces études portent sur des gestes dirigés soit vers des humains soit à la fois des humains et des conspécifiques (données regroupées) mais jamais des gestes dirigés uniquement vers des conspécifiques.

À notre connaissance, aucune étude n'a précédemment étudié la latéralité manuelle:

1. en prenant simultanément en compte les influences potentielles de plusieurs facteurs et de leurs interactions, point essentiel pour éviter des biais générateurs de résultats ambigus et également condition nécessaire pour estimer l'effet particulier d'une fonction (par exemple non-communication vs communication),
2. en étudiant les effets des facteurs sociodémographiques sur la latéralité en considérant plusieurs catégories étroites d'âge (par exemple immatures, adolescents, jeunes et matures adultes) ainsi que de rang hiérarchique (par exemple dominants, intermédiaires et subordonnés), points essentiels pour appréhender au mieux les effets particuliers à chaque modalité des variables sociodémographiques considérées,
3. en considérant les caractéristiques sociodémographiques non seulement des émetteurs mais également des récepteurs,
4. en considérant la communication purement intraspécifique (seule appropriée du point de vue de l'évolution) ainsi que l'utilisation d'outils (considérée selon certaines hypothèses comme ayant facilité l'émergence du langage humain (e.g. Forrester et al. 2013)) pour comparer la latéralité manuelle entre manipulation et communication.

La présente thèse de doctorat avait les trois objectifs suivants. Le premier objectif était de fournir une analyse détaillée de la latéralité gestuelle chez deux proches parents des humains, les chimpanzés et les gorilles, en étudiant la production des gestes les plus fréquents de leurs répertoires spécifiques naturels. Le deuxième objectif était de comparer nos résultats entre ces deux espèces. Pour atteindre ces deux premiers objectifs, nous avons évalué la latéralité intraspécifique au cours d'interactions dyadiques en considérant trois groupes de chimpanzés (*Pan troglodytes spp.*) (N = 39) et trois groupes de gorilles (*Gorilla gorilla gorilla*) (N = 35) vivant dans des conditions favorables de captivité. Pour chaque espèce, nous

avons conçu et appliqué des procédures d'observation et d'analyses statistiques afin d'évaluer leur latéralité gestuelle à l'échelle de la population, de même que pour évaluer et comparer l'influence respective sur la latéralité gestuelle de trois catégories de facteurs: les composantes liées aux contextes des interactions sociales (champs visuels et côtés du corps de l'émetteur et du receveur, la valence émotionnelle du contexte), le type de geste (modalité sensorielle, utilisation d'outil de communication, durée, degré de partage au sein de la population) et différentes caractéristiques sociodémographiques de l'émetteur et du receveur (âge, sexe, groupe, hiérarchie, parenté et affiliation). Le troisième objectif de cette thèse était de chercher à savoir si les composantes de manipulation et de communication sont contrôlées par le même système cérébral latéralisé dans l'hémisphère gauche. Pour ce faire, nous avons comparé la latéralité manuelle des chimpanzés lors de l'utilisation d'outil dans des gestes intraspécifiques et dans des actions non-communicatives semblables à la pêche aux termites. Nous avons d'abord évalué la latéralité manuelle au niveau de la population pour ces comportements puis nous avons étudié l'influence des différentes caractéristiques sociodémographiques pour les fonctions de communication et de non-communication.

II - Résultats & Discussion

Dans une perspective comparative, nous discutons ci-dessous les principaux résultats de nos études aux regards des structures et dynamiques sociales des chimpanzés et des gorilles, de même qu'aux regards des implications de ces résultats sur les origines évolutives de la latéralité à l'échelle de la population et du langage humain. Tout d'abord, nous discutons nos résultats liés à la latéralité manuelle au niveau populationnel en considérant les gestes intraspécifiques des chimpanzés et des gorilles, puis les gestes intraspécifiques et les actions non-communicatives des chimpanzés impliquant l'utilisation d'outils. Ensuite, nous discutons les résultats de notre étude multifactorielle sur la latéralité manuelle pour ces différents comportements. Pour finir, nous concluons et présentons les implications de nos résultats sur les origines évolutives de la latéralisation hémisphérique cérébrale chez l'humain. Nous proposons également quelques directions pour de futures recherches.

1. Latéralité manuelle au niveau populationnel

1.1. Latéralité gestuelle chez les chimpanzés et les gorilles

En considérant la latéralité sur un continuum (e.g. McGrew & Marchant 1997), nous avons montré que les chimpanzés (respectivement les gorilles) présentaient un biais manuel à

droite au niveau de la population pour la majorité (13 sur 21) (respectivement 9 sur 16) de leurs gestes intraspécifiques les plus fréquents. D'un point de vue comparatif, il est intéressant de noter que 8 des 14 gestes les plus fréquemment utilisés par les deux espèces ont présenté un biais droit au niveau de la population (i.e. SLAP HAND, EMBRACE, PUNCH, THROW OBJECT, ATTEMPT TO REACH, PUT OBJECT ON HEAD, SHAKE OBJECT and RAISE ARM).

La direction des asymétries de la plupart des espèces est généralement semblable pour la majorité des individus d'une population (60 à 90% selon les espèces et les comportements considérés) (e.g. Bisazza et al. 1998; Vallortigara et al. 1999, 2005; Rogers 2002; Vallortigara & Bisazza 2002). Ghirlanda et collègues (2009) ont récemment mis en évidence que des nombres inégaux d'individus latéralisés à gauche et à droite dans les populations peuvent être expliqués par une stratégie évolutive stable (SES) basée sur un compromis entre les interactions intraspécifiques compétitives et coopératives. Nos résultats concernant la latéralité gestuelle intraspécifique des chimpanzés et des gorilles soutiennent le modèle de Ghirlanda et collègues (2009). De plus, suite à nos résultats nous pouvons supposer que l'ancêtre commun aux chimpanzés et aux gorilles aurait eu une préférence pour l'utilisation de la main droite au moins pour les 8 gestes mentionnés ci-dessus. Cette hypothèse est confortée par d'autres études chez les chimpanzés et les singes qui mettent en évidence un biais manuel à droite au niveau de la population :

- pour les gestes intraspécifiques chez les chimpanzés en captivité (pour une catégorie de gestes regroupant THREAT, EXTEND ARM et HAND SLAP: Meguerditchian et al. 2010a) et en milieu naturel (pour une catégorie de gestes qui impliquent l'utilisation d'un objet et regroupant OBJECT SHAKE et OBJECT MOVE: Hobaiter & Byrne 2013), de même que chez les babouins olives pour HAND SLAP (Meguerditchian & Vauclair 2006),
- pour les gestes dirigés vers des humains tels que ceux produits par les chimpanzés (e.g. FOOD BEG: Hopkins & Leavens 1998; CLAPPING: Meguerditchian et al. 2012) et les babouins olives (POINTING: Meunier et al. 2012; HAND SLAP: Meguerditchian & Vauclair 2006),
- pour THROW OBJECT dirigé vers des humains et des conspécifiques (données regroupées) chez les chimpanzés (Hopkins et al. 2005b).

En mettant en évidence un biais manuel à droite au niveau de population pour la majorité des gestes intraspécifiques les plus fréquemment produits par les chimpanzés et les gorilles dans divers contextes sociaux, les résultats de cette thèse ainsi que ceux des trois études mentionnées ci-dessus (chimpanzés: Meguerditchian et al. 2010a; Hobaiter & Byrne 2013; babouins: Meguerditchian & Vauclair 2006) montrent qu'un tel biais est présent dans la

communication strictement intraspécifique et non pas limité à la communication interspécifique. Plus généralement, les résultats de cette thèse sont en accord avec un nombre grandissant d'articles montrant une prédominance de l'utilisation de la main droite dans la communication gestuelle de certains primates et suggérant que la latéralité gestuelle serait un précurseur de la spécialisation de l'hémisphère gauche pour le langage.

Les chimpanzés (respectivement les gorilles) n'ont pas montré de biais manuel à droite pour 8 des 21 (respectivement 7 des 16) autres gestes considérés. Nous n'avons pas mis en évidence de biais manuel à droite au niveau de la population pour quatre des 14 gestes fréquents produits par les deux espèces (i.e. EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, and TOUCH BODY) (toutefois, nous avons trouvé une tendance pour l'utilisation de la main droite chez les gorilles pour EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL). L'absence de biais significatif au niveau de la population pour des gestes tactiles a également été montrée par deux autres études ayant étudié la latéralité dans la communication strictement intraspécifique, chez les chimpanzés pour TOUCH OTHER et EMBRACE (Fletcher & Weghorst 2005) et chez les bonobos pour TOUCH BODY, TOUCH GENITAL, EMBRACE LATERAL et MOVING WITH ARMS AROUND THE PARTNER (même geste que EMBRACE HALF mais nommé différemment) (Chapelain 2010). Ces résultats suggèrent que la modalité sensorielle pourrait moduler la latéralité gestuelle intraspécifique des chimpanzés et des gorilles, un effet qui a été montré par notre étude multifactorielle.

1.2. Latéralité manuelle lors de l'utilisation d'outil par des chimpanzés dans des actions non-communicatives et dans des gestes intraspécifiques

Nous avons comparé la latéralité manuelle lors de l'utilisation d'outil par des chimpanzés dans des actions non-communicatives semblables à la pêche aux termites (e.g. McGrew & Marchant 1992) et dans des gestes intraspécifiques. En considérant la latéralité sur un continuum, nous avons mis en évidence un biais manuel à droite au niveau populationnel pour chacun des cinq gestes dirigés vers des conspécifiques impliquant l'utilisation d'un outil, mais pas pour les actions non-communicatives impliquant l'utilisation d'un d'outil.

Les résultats pour les actions non-communicatives impliquant l'utilisation d'un d'outil sont en accord avec l'étude de Hopkins et collègues (2009) qui n'a pas mis en évidence de biais manuel au niveau de la population chez les chimpanzés captifs pour une tâche nécessitant l'utilisation d'outil conçue pour simuler la pêche aux termites. Cependant, nos

résultats ne sont pas en accord avec ceux des études ayant été menées sur des chimpanzés sauvages pour la pêche aux termites (Bogart et al. 2012; Lonsdorf & Hopkins 2005; McGrew & Marchant 1992, 1996, 1999) montrant un biais manuel à gauche au niveau populationnel. Nous avons émis l'hypothèse que les différences entre ces études et la nôtre pourraient être attribuées en partie 1) aux effets des facteurs génétiques et/ou de l'apprentissage social sur la latéralité comme proposé par Lonsdorf et Hopkins (2005) afin d'expliquer les variations de la direction de la latéralité (liées à la spécificité de tâches impliquant l'utilisation d'un outil) entre des groupes de chimpanzés sauvages, 2) aux différences d'exigences haptiques et sensorielles pendant l'insertion et l'extraction de l'outil (Hopkins et al. 2009) entre nos actions non-communicatives et la pêche aux termites dans le milieu naturel.

Les résultats concernant chacun des cinq gestes intraspécifiques impliquant l'utilisation d'un outil de communication concordent avec ceux de précédentes études montrant également un biais de latéralité manuelle à droite pour des gestes impliquant l'utilisation d'un outil de communication, dirigés vers des conspécifiques chez des chimpanzés sauvages (Hobaiter & Byrne 2013) et dirigés vers des humains (Hopkins et al. 1993) et vers des humains et des conspécifiques (données regroupées) (Hopkins et al. 2005b) chez des chimpanzés captifs. Tous ces résultats concernant les gestes effectués par des chimpanzés impliquant un outil de communication confortent la théorie de l'origine gestuelle du langage humain (e.g. Corballis 2002, 2003) proposant que la latéralité gestuelle serait un précurseur de la spécialisation de l'hémisphère gauche pour le langage.

Les mécanismes/facteurs sous-jacents à la latéralité manuelle dans les gestes et la manipulation sont discutés ci-dessous à la lumière de notre analyse multifactorielle.

2. Etude multifactorielle de la latéralité manuelle

Le fait de considérer plusieurs catégories de gestes plutôt que de limiter notre analyse à l'étude de gestes distincts nous a permis d'explorer la latéralité gestuelle de manière approfondie. Pour aller plus loin dans notre analyse, nous avons pris en compte simultanément de multiples facteurs susceptibles d'influencer la latéralité gestuelle. Nous avons montré que la latéralité gestuelle intraspécifique des chimpanzés et des gorilles étudiés était influencée par plusieurs facteurs et par leurs interactions mutuelles: le contexte interactionnel (champs visuels de l'émetteur et du receveur ainsi que la valence émotionnelle liée à l'interaction sociale), le type de gestes (modalité sensorielle, utilisation d'un outil de communication, degré de partage au sein de la population et durée du geste) et par certaines

caractéristiques sociodémographiques, en particulier le rang hiérarchique de l'émetteur et, dans une moindre mesure, l'âge de l'émetteur. Les analyses ont révélé des similitudes mais également des différences entre les deux espèces. Plus précisément, les chimpanzés émetteurs ont utilisé leur main ipsilaterale au receveur pour des gestes tactiles et visuels, et leur main contralatérale pour des gestes auditifs et ceux impliquant l'utilisation d'un outil de communication. L'utilisation de la main droite par les chimpanzés émetteurs était plus importante pour les gestes communs effectués dans des contextes émotionnels négatifs et pour les gestes tactiles effectués par les subordonnés. Les gorilles émetteurs ont utilisé leur main ipsilaterale au receveur pour produire les gestes tactiles et visuels, et quel que soit le contexte émotionnel, la durée du geste, le sexe du receveur, le lien de parenté entre l'émetteur et le receveur et le fait d'utiliser un outil de communication ou non. Les gorilles émetteurs n'ont pas préférentiellement utilisé leur main contralatérale quelle que soit la situation. L'utilisation de la main droite par les gorilles émetteurs a été particulièrement marquée dans les contextes négatifs, pour effectuer des gestes courts, de même que pour les femelles émettrices. De plus, son utilisation augmentait avec l'âge.

Dans le cadre d'une approche comparative entre les chimpanzés et les gorilles, nous discutons nos résultats en considérant, tout d'abord, les facteurs ayant été trouvés sans effet sur la latéralité gestuelle des chimpanzés et des gorilles, puis nos résultats concernant la latéralisation du traitement des émotions lié aux gestes ainsi que la modulation de latéralisation des gestes par des stratégies de communication et par des pressions sociales de sélection. Ensuite, en considérant la latéralité manuelle des chimpanzés en contexte d'utilisation d'outil dans la communication gestuelle intraspécifique et la manipulation, nous aborderons les effets de l'âge, du sexe et de la hiérarchie, ceci nous permettant d'apprécier les effets de la fonction (communicative et non-communicative) en tant que telle. En conclusion, nous commentons nos résultats par rapport aux théories sur les origines évolutives de la latéralisation hémisphérique cérébrale humaine puis nous proposons également quelques directions pour de futures recherches.

2.1. Facteurs sans effet sur la latéralité gestuelle des chimpanzés et des gorilles

Les résultats concernant les chimpanzés et les gorilles n'ont pas mis en évidence d'influence significative de la parenté, du sexe et de la hiérarchie du receveur sur l'utilisation de la main droite des émetteurs. Il est intéressant de noter que ces facteurs sans effet concernent seulement les caractéristiques des receveurs. Contrairement à ce que l'on avait

initialement pensé, les résultats suggèrent que les caractéristiques des receveurs n'ont pas joué un rôle déterminant sur la latéralité gestuelle des chimpanzés et des gorilles.

2.2. Latéralisation du traitement des émotions lié aux gestes

Les résultats ont suggéré que l'état émotionnel des émetteurs (valence émotionnelle en tant que telle et états émotionnels liés au stress) affecterait leur latéralité gestuelle via la valence émotionnelle liée à l'interaction sociale (positive ou négative), le statut hiérarchique de l'émetteur, les expressions faciales des émotions des receveurs (plus prononcées sur leur hémiface gauche que sur leur hémiface droite).

Concernant la valence émotionnelle, nous avons constaté que les gorilles émetteurs utilisaient particulièrement plus leur main droite dans des contextes négatifs. Ce constat fut également observé chez les émetteurs chimpanzés pour les gestes communs (gestes exprimés par la majorité des individus de la population considérée). Ces résultats sont en accord avec la revue de littérature de Rohlfs et Ramirez (2006) soulignant l'importance de distinguer la valence émotionnelle (positive-négative) et la motivation d'approche et de retrait et mettant en évidence que la « colère » (de valence négative (e.g. Lazarre 1991) et qui suscite fréquemment une motivation d'approche (e.g. Berkowitz 1999)) augmente l'activité du cerveau préfrontal chez l'humain conduisant en une utilisation préférentielle de la main droite en contextes émotionnels négatifs (e.g. Harmon-Jones 2004).

Concernant le statut hiérarchique des émetteurs, les résultats ont montré que les chimpanzés et les gorilles subordonnés étaient globalement plus droitiers que les individus de rang hiérarchique intermédiaire. De plus, les chimpanzés subordonnés étaient globalement plus droitiers que les dominants. Ces différences pourraient être la conséquence d'un niveau de stress psychosocial plus élevé (e.g. compétition pour l'accès à la nourriture et à l'espace) subit par les individus subordonnés menant à une plus grande utilisation de la main droite; il est à noter que la captivité pourrait aggraver le stress psychosocial (Muller & Wrangham 2004). En effet, le stress provoquerait un biais de latéralité des membres à droite au niveau de la population (rats: e.g. Alonso et al. 1991; Castellano et al. 1987, 1989; anoles: Deckel 1998) probablement parce qu'il inhiberait l'hémisphère droit (associé au côté gauche du corps). Cette hypothèse est soutenue par la revue de littérature de Rohlfs et Ramirez (2006) chez les humains. Contrairement à nos résultats sur les chimpanzés, les gorilles subordonnés n'étaient pas plus droitiers que les dominants. Cette différence pourrait être due à la structure sociale des gorilles qui vivent en harems polygynes contrôlés par un mâle mature dominant (e.g. Gatti

et al. 2004). La compétition pour la reproduction pourrait induire un certain niveau de stress chez les gorilles de haut rang (constitué en majorité de femelles): le stress psychosocial provoqué par la stratégie de reproduction adoptée par les femelles de haut rang, en particulier les femelles de Vallée des Singes (observations personnelles), pourrait augmenter l'utilisation de la main droite, conformément à l'hypothèse précédemment émise.

Concernant la perception des expressions faciales des émotions des receveurs, les résultats ont indiqué que les chimpanzés et les gorilles émetteurs étaient globalement plus droitiers lorsqu'ils étaient situés dans le champ visuel gauche des receveurs pendant l'interaction sociale (RVF_L) que dans le champ visuel droit des receveurs (RVF_R). Nous avons supposé que les expressions faciales des émotions des receveurs plus prononcées sur l'hémiface gauche que sur l'hémiface droit (e.g. chimpanzés: Wallez et al. 2012; macaques rhésus: Hauser 1993; babouins: Wallez & Vauclair 2011; humains: Nicholls et al. 2002) pourrait augmenter l'état émotionnel des émetteurs durant l'interaction. Ceci expliquerait donc une plus grande utilisation de la main droite par les émetteurs en situation RVF_L. En effet, comme détaillé précédemment, les émotions et le stress pourraient moduler l'utilisation de la main droite.

2.3. Latéralisation des gestes: modulation par des stratégies de communication

D'après nos résultats, les chimpanzés et les gorilles utiliseraient des stratégies de communication différentes selon le type de gestes (i.e. tactile, visuel ou auditif; gestes impliquant ou pas l'utilisation d'un outil de communication).

En ce qui concerne la modalité sensorielle des gestes, les chimpanzés et les gorilles utilisaient plus leur main droite pour produire des gestes tactiles (impliquant un contact physique avec le receveur) et les gestes visuels (impliquant la transmission d'un signal visuel) lorsque le receveur était situé dans leur champ visuel droit pendant l'interaction (SVF_R) que dans leur champ visuel gauche (SVF_L). Nous avons émis l'hypothèse qu'ils ont utilisé la main ipsilaterale au receveur afin de faciliter la transmission de ces signaux tactiles et visuels. Contrairement aux gestes tactiles et visuels, les chimpanzés émetteurs ont utilisé préférentiellement leur main du côté opposé au receveur (i.e. main contralatérale) pour produire les gestes auditifs. Nos observations nous ont conduits à émettre l'hypothèse que lorsqu'ils prévoient de produire un geste auditif, ils laissent libre leur main proche du receveur afin de pouvoir l'utiliser pour d'éventuels futurs gestes tactiles ou visuels dirigés vers le receveur (e.g. pour effectuer un PUSH).

Concernant les gestes impliquant l'utilisation d'un outil de communication, les chimpanzés et gorilles émetteurs ont plus utilisé leur main droite pour des gestes avec objet que pour des gestes sans objet lorsque le receveur était dans leur champ visuel gauche (SVF_L). En d'autres termes, ils ont utilisé préférentiellement leur main contralatérale au receveur pour communiquer avec un objet. A partir d'observations personnelles, nous avons émis l'hypothèse qu'ils agissaient ainsi probablement pour empêcher le receveur de saisir l'objet (potentiellement convoité) utilisé comme outil de communication et/ou pour laisser libre leur main ipsilaterale au receveur afin de pouvoir l'utiliser pour effectuer un éventuel futur geste dirigé vers ce dernier.

2.4. Latéralisation des gestes: modulation par des pressions de sélection en lien avec la structure et la dynamique sociale

D'après la théorie sociale de l'origine de la latéralité (Ghirlanda & Vallortigara 2004 ; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009), l'alignement de la latéralité au niveau populationnel pourrait être le résultat de pressions sociales.

Nos comparaisons inter-espèces ont suggéré que les pressions sociales de sélection pourraient avoir agi sur la latéralité gestuelle de nos deux proches parents que sont les chimpanzés et les gorilles. En effet, nous avons émis l'hypothèse que la structure et la dynamique sociale de ces espèces ont modulé différemment l'influence des facteurs tel que : la modalité sensorielle et le degré de partage des gestes ainsi que le rang hiérarchique, le sexe, l'âge et le groupe des individus émetteurs, sur la latéralité gestuelle.

La modalité sensorielle des gestes. Les chimpanzés émetteurs ont globalement plus utilisé leur main droite pour produire les gestes visuels que les gestes tactiles et auditifs. De plus, ils ont globalement plus utilisé leur main droite pour produire les gestes tactiles que les gestes auditifs. Au contraire, les gorilles émetteurs ont globalement plus utilisé leur main droite pour produire les gestes auditifs que pour les gestes visuels et tactiles. Dans leur revue, Pika et collègues (2005b) ont mentionné que les gestes auditifs représentent une plus grande partie (environ un cinquième) du répertoire des gorilles que de celui des chimpanzés (environ un dixième). Comme les gestes auditifs sont plus communs chez les gorilles, on peut supposer que ces gestes seraient plus codifiés/latéralisés chez les gorilles que chez les chimpanzés, ceci pour une meilleure coordination sociale.

Le degré de partage des gestes. Nous avons mis en évidence qu'il influençait l'utilisation de la main droite seulement pour les chimpanzés. Les chimpanzés émetteurs ont

globalement plus utilisé leur main droite pour produire des gestes communs que des gestes rares, probablement du fait du bénéfice apporté par une plus forte codification/latéralisation des gestes communs que des gestes rares. Ceci aurait pour conséquence de créer une meilleure coordination sociale qui faciliterait les interactions et donc la cohésion sociale. Nous supposons que cette facilitation de cohésion pourrait être particulièrement bénéfique chez les chimpanzés vivant dans des groupes caractérisés par une plus forte variabilité d'association par rapport aux gorilles qui vivent généralement dans des groupes cohésifs (Aureli et al. 2008).

Le rang hiérarchique des émetteurs. Conformément à l'hypothèse précédemment émise (voir ci-dessus la discussion portant sur la latéralisation du traitement émotionnel lié aux gestes), les différences de patterns de latéralité entre les gorilles et les chimpanzés pourraient être dues à la stratégie de compétition pour l'accès à la reproduction des femelles gorilles de haut rang hiérarchique.

Le sexe des émetteurs. Les femelles gorilles étaient globalement plus droitières que les mâles. Au contraire, nos résultats relatifs aux chimpanzés n'ont pas mis en évidence d'effet du sexe des émetteurs sur l'utilisation de leur main droite. Au regard de la structure sociale spécifique des gorilles, nous supposons que la compétition pour la reproduction entre les femelles induirait un certain niveau de stress psychosocial (en particulier parmi les femelles de haut rang hiérarchique) qui augmenterait l'utilisation de la main droite (voir ci-dessus la discussion portant sur la latéralisation du traitement émotionnel lié aux gestes). D'autres recherches sont nécessaires afin de mieux comprendre l'influence du sexe sur la latéralité gestuelle des primates.

L'âge des émetteurs. Nos résultats ont indiqué que les enfants gorilles étaient plus droitiers pour produire des gestes dirigés vers des adultes matures que vers de jeunes adultes. Cependant, chez les chimpanzés, nous n'avons pas mis en évidence d'effet de l'âge des receveurs sur l'utilisation de la main droite des émetteurs. Cette différence entre les deux espèces pourrait être due à l'effet du stress psychosocial mentionné ci-dessus, éprouvé par les enfants gorilles émetteurs interagissant avec les gorilles matures. En fait, le harcèlement des mères, et plus spécialement de leurs nourrissons, par les autres femelles est apparu comme étant plus agressif au sein des groupes de gorilles (particulièrement au Burgers' zoo) que des groupes de chimpanzés considérés (observations personnelles). Ce type de compétition reproductive pourrait être exacerbé chez les gorilles en raison de leur structure sociale en harem polygyne.

L'effet du groupe. Nous avons mis en évidence cet effet sur l'utilisation de la main droite des gorilles émetteurs. Ces différences entre les groupes/zoos pourraient être dues aux pressions sociales proposées pour expliquer des différences de latéralité entre groupes sociaux pour des activités communicatives (Ghirlanda & Vallortigara 2004; Vallortigara & Rogers 2005; Vallortigara 2006; Ghirlanda et al. 2009). Cependant, nos résultats relatifs aux chimpanzés n'ont pas mis en évidence de différence aussi claire entre les groupes/zoos: des différences dans l'utilisation de la main droite des chimpanzés émetteurs n'ont été trouvées qu'entre deux groupes, et ce, uniquement lors de la production de gestes auditifs. Nous avons émis l'hypothèse que la structure sociale des gorilles, organisée autour d'un unique individu (i.e. le mâle dominant), serait plus à même de provoquer des différences de latéralité gestuelle entre les groupes que la structure sociale des chimpanzés organisée en petits sous-groupes d'individus sujets à un degré élevé de dynamique fission-fusion. À cette cause distale pourrait aussi s'ajouter une cause proximale liée aux rapports du nombre adultes mâles-adultes femelles qui diffèrent davantage entre les groupes de gorilles (La Vallée: 0,33; Apenheul: 0,25; Burgers' zoo: 0,5) qu'entre les groupes de chimpanzés (Leipzig, Beauval, La Palmyre: 0,25). De futures comparaisons entre d'autres groupes de gorilles et de chimpanzés, de même qu'entre d'autres espèces vivant en harems et en groupes multi-mâle/multi-femelles sont nécessaires pour confirmer ces hypothèses.

2.5. Latéralisation des gestes et de la manipulation manuelle : modulation par des facteurs sociodémographiques

Notre étude multifactorielle a démontré un effet de l'âge sur la latéralité manuelle en contexte de communication aussi bien que de non-communication. Nos résultats confortent des études précédentes (e.g. McGrew & Marchant 1997) montrant une préférence manuelle plus marquée avec l'âge et proposant ainsi que la préférence manuelle pourrait être une conséquence de la maturation et/ou de l'apprentissage et de l'expérience. Cependant, nous avons trouvé une diminution de l'usage de la main droite chez les chimpanzés plus âgés probablement due aux limitations physiques et à une activité plus réduite (documentées chez les humains: e.g. Hughes et al. 1997) et/ou à une moindre socialité, liées au vieillissement, qui pourraient diminuer les performances de la main droite (performances résultant de la pratique), celles-ci convergeant donc vers celles de la main gauche. Ceci pourrait être un effet de la sénescence, mis en évidence pour la première fois sur la latéralité manuelle des primates non-humains). L'influence du sexe des émetteurs sur l'utilisation de la main pour les gestes et

la manipulation demeure, en revanche, peu claire. Des recherches complémentaires sont nécessaires afin de mieux comprendre l'influence du sexe sur la latéralité gestuelle des primates.

L'interprétation de l'effet du rang hiérarchique des émetteurs sur la latéralité manuelle des chimpanzés lors de l'utilisation d'outil en contexte de communication aussi bien que de non-communication, a suggéré qu'un effet de stress psychosocial augmenterait l'utilisation de la main droite dans la manipulation. Or nous avons trouvé que les chimpanzés dominants (potentiellement exempts de stress psychosocial et de contraintes haptiques liées à l'utilisation d'outil en vue d'obtenir de la nourriture) utilisaient plus la main droite pour les gestes que pour les manipulations. Ce résultat conforte donc l'hypothèse que certains primates ainsi que les enfants en bas âge ont un traitement spécifique de la communication gestuelle, par leur hémisphère cérébral gauche, distinct de celui impliqué dans les actions manuelles non-communicatives (e.g. Meguerditchian & Vauclair 2009).

2.6. Conclusion générale et propositions de futures recherches

Pour conclure, notre thèse apporte des contributions significatives quant aux implications concernant l'origine évolutive de la latéralité au niveau populationnel ainsi que du langage humain. Notre étude a d'une façon convaincante prouvé que nos chimpanzés et gorilles étaient droitiers au niveau populationnel pour la majorité des gestes les plus fréquents de leurs répertoires naturels respectifs de communication (parmi lesquels 8 gestes fréquents communs aux deux espèces). C'est à notre connaissance la première mise en évidence d'un biais au niveau populationnel pour les gestes purement intraspécifiques chez les gorilles. Notre approche multifactorielle a montré pour la première fois chez des primates que la latéralité dans la communication gestuelle et dans la manipulation était modulée par plusieurs facteurs et leurs interactions. Concernant la communication gestuelle purement intraspécifique, la latéralité des gestes les plus fréquemment exprimés par les chimpanzés et les gorilles a été particulièrement modulée par les caractéristiques associées au contexte de l'interaction (champs visuels des émetteurs et des récepteurs ainsi que contexte émotionnel), par le type de geste (modalité sensorielle, utilisation d'un outil de communication et degré de partage) et par les composantes sociodémographiques, particulièrement le rang hiérarchique de l'émetteur et, dans une moindre mesure, l'âge du récepteur. Nos résultats ont montré des similitudes et des différences entre les deux espèces qui peuvent être liées 1) à la latéralisation du traitement de l'émotion (valence émotionnelle en tant que telle et stress lié à l'état

émotionnel de l'émetteur), 2) à la latéralisation des gestes en fonction de différentes stratégies de communication selon le type de geste exécuté par les chimpanzés et les gorilles, et 3) à la latéralisation des gestes, résultat de pressions sociales de sélection liées à la structure et la dynamique sociales des espèces étudiées. Considérant maintenant à la fois les contextes de communication et de non-communication, nos analyses multifactorielles ont montré un effet des caractéristiques sociodémographiques individuelles sur la latéralité manuelle de ces primates avec la première mise en évidence d'un effet de la sénescence et d'un effet du rang hiérarchique. Nos résultats concernant l'influence du sexe des émetteurs sur la latéralité des gestes et sur la manipulation sont toutefois moins clairs et des études complémentaires seraient nécessaires pour une meilleure compréhension de ces effets et de leurs causes déterminantes.

En conclusion, nos résultats relatifs aux chimpanzés nous conduisent à émettre l'hypothèse que la prédominance de la main droite chez les primates pour les gestes sans utilisation d'outil (qui impliquent donc seulement une composante de communication) serait plus marquée que pour des gestes avec outil (qui impliquent à la fois des composantes de communication et de manipulation), laquelle serait elle-même plus marquée que pour les actions non-communicatives avec outil. Bien que les actions non-communicatives avec outil puissent induire une forte latéralité, nous n'avons pas mis en évidence de biais en faveur de la main droite au niveau populationnel. Par conséquent, nos résultats globaux ne confortent qu'en partie l'hypothèse de l'utilisation d'outil (e.g. Greenfield 1991; Forrester et al. 2013) selon laquelle les conditions sensorimotrices particulières requises par l'utilisation d'outil aussi bien pour les activités de communication que non-communicatives auraient induit une forte préférence pour l'utilisation de la main droite. Cependant, il serait nécessaire de tester ces hypothèses en considerant d'autres actions non-communicatives spontanées avec outil telles que « wadge dipping » (Boesch 1991). D'autres études sont donc nécessaires pour confirmer si l'utilisation d'outil pourrait avoir constitué une pression de sélection qui aurait déterminé l'émergence des deux manifestations les plus prononcées de la spécialisation hémisphérique des humains que sont la préférence manuelle à droite pour la manipulation et la spécialisation de l'hémisphère gauche pour le langage.

En conclusion, notre étude sur la latéralité gestuelle intraspécifique des chimpanzés et des gorilles vérifie globalement le modèle de Ghirlanda et collègues (2009) selon lequel les biais au niveau populationnel seraient expliqués par une Stratégie Evolutive Stable basée sur les interactions intraspécifiques. De plus, nos résultats vont dans le sens de la théorie sur l'origine gestuelle du langage (e.g. Corballis 2002, 2003) proposant que la latéralité gestuelle

représente un précurseur de la spécialisation cérébrale gauche pour le langage. En outre, nos résultats relatifs à la latéralité manuelle des chimpanzés pour l'usage d'outil dans les gestes intraspécifiques et la manipulation confortent l'hypothèse que certaines espèces de primates auraient un traitement spécifique de l'hémisphère gauche pour la communication gestuelle distinct de celui utilisé pour les actions manuelles non-communicatives (e.g. Meguerditchian & Vauclair 2009).

Afin d'approfondir notre compréhension des origines évolutives de la latéralité au niveau populationnel ainsi que du langage humain, de futures études devront :
1) considérer des contextes socioécologiques représentatifs des conditions dans lesquelles la sélection naturelle a opéré, c'est à dire dans lesquels les sujets interagissent avec des conspécifiques dans un environnement tel que: vie sauvage et/ou captivité avec naturalisation optimale des enclos et groupes sociaux incluant un nombre suffisant de sujets,
2) étudier la latéralité gestuelle intraspécifique (seule appropriée dans une perspective évolutive) des humains et d'autres proches parents (i.e. grands singes: bonobos et orangs-outans), ainsi que des singes avec des structures sociales, une dynamique et des degrés de socialité différents,
3) effectuer une collecte des données et une analyse appropriée de celles-ci: échantillon d'individus suffisamment nombreux, grand nombre de données par sujet, indépendance des données, prise en compte de multiples facteurs potentiellement influents et analyse statistique permettant d'estimer les influences respectives de ces facteurs et de leurs interactions.

Une telle méthodologie devrait nous permettre de mieux comprendre les sources de disparités entre les études et entre les espèces.

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Le Directeur de Thèse Doctorale

(Nom et Prénom)

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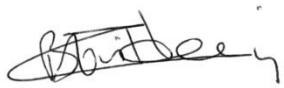

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Chimpanzees' and gorillas' intraspecific gestural laterality: a multifactorial investigation

We studied intraspecific gestural laterality of captive chimpanzees and gorillas in real-life social-ecological relevant contexts. We evidenced that chimpanzees (respectively gorillas) exhibited a right-hand bias at the population level for the majority of the most frequent gestures of their specific natural communication repertoire. By designing and applying a multifactorial approach, we showed for the first time that intraspecific gestural laterality of primates was influenced by several factors and their mutual intertwinement: interactional context (visual fields of both signaller and recipient as well as emotional context), gesture characteristic (sensory modality, use of a communication tool, sharing degree, and gesture duration) and by some socio-demographic components in particular signaller's hierarchical rank, and to a lesser extent signaller's age. Similarities but also some discrepancies between chimpanzees and gorillas may be related to the lateralization of emotional processing, to communication strategies, and to social selection pressures related to the social structure and dynamics of the study species. Moreover, we compared manual laterality of tool use by chimpanzees in both non-communication actions and intraspecific gestures. Our multifactorial analysis showed that tool-use in gestures appear to be governed more by the left cerebral hemisphere than tool-use in non-communication actions. Our findings support Ghirlanda and colleagues' (2009) model postulating that population-level bias could be explained by an evolutionary stable strategy based on intraspecific interactions. Our results also agree with previous reports evidencing predominant right-hand use by nonhuman primates for gestural communication and suggesting that gestural laterality would be a precursor of the left-brain specialization for language. Furthermore, our results support the hypothesis that some primate species may have a specific left cerebral system processing gestures distinct from the cerebral system processing non-communication manual actions. From an evolutionary point of view, our findings emphasize the importance to study intraspecific laterality in detail by considering species varying in their degree of sociality and taking into account real-life social-ecological contexts and multiple potentially influential factors.

Latéralité gestuelle intraspécifique chez les chimpanzés et les gorilles: une étude multifactorielle

Nous avons étudié la latéralité gestuelle intraspécifique de chimpanzés et de gorilles captifs dans des contextes socio-écologiques proches des conditions naturelles de vie. Nous avons montré que les chimpanzés et les gorilles étudiés présentaient un biais populationnel pour la main droite pour la majorité des gestes les plus fréquents de leur répertoire. Par la mise en œuvre d'une approche multifactorielle, nous avons montré pour la première fois que la latéralité gestuelle intraspécifique de ces primates était influencée par plusieurs facteurs et par leurs interactions: contexte de l'interaction (champs visuels de l'émetteur et du récepteur et contexte émotionnel), caractéristique du geste (modalité sensorielle, utilisation d'un outil de communication, degré de partage et durée du geste) et par certaines composantes sociodémographiques, particulièrement le rang hiérarchique de l'émetteur et son âge dans une moindre mesure. De plus, nous avons comparé la latéralité manuelle des chimpanzés lors de l'utilisation d'outil pour des actions non-communicatives et des gestes intraspécifiques. Notre analyse multifactorielle suggère que l'utilisation d'outil dans les gestes serait plus contrôlée par l'hémisphère cérébral gauche que l'utilisation d'outil dans des actions non-communicatives. Globalement, nos résultats vérifient le modèle de Ghirlanda et collègues (2009) selon lequel les biais de latéralité au niveau populationnel pourraient être expliqués par une stratégie évolutive stable basée sur les interactions intraspécifiques. Nos résultats sont également en accord avec les études mettant en évidence l'utilisation préférentielle de la main droite pour la communication gestuelle des primates non humains et suggérant que la latéralité gestuelle serait un précurseur de la spécialisation hémisphérique gauche pour le langage. En outre, nos résultats confortent l'hypothèse que certaines espèces de primates pourraient avoir un traitement spécifique de l'hémisphère gauche pour les gestes communicatifs distinct de celui des actions manuelles non-communicatives. Du point de l'évolution, nos résultats soulignent l'importance d'étudier en détail la latéralité intraspécifique en considérant des espèces de différents degrés de socialité et en prenant en compte des contextes socioécologiques proches des conditions naturelles ainsi que de multiples facteurs potentiellement influents.