



Do Mechanical Effectiveness and Recipient Species Influence Intentional Signal Laterality in Captive Chimpanzees (*Pan troglodytes*)?

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Abstract

Studying the relationships between the directions of brain lateralization for handedness and language can shed light on mechanisms underlying hemispheric specialization for manipulation and signalling functions. We investigated the influence of manipulation and communication functions and of recipient species (conspecific- versus human-directed communication) on manual laterality in signalling context, taking several factors into account simultaneously. We assessed laterality in 39 chimpanzees (*Pan troglodytes*), including 4 manipulators (mechanically effective social actions used to get things done) and 18 gestures (mechanically ineffective social actions implying that the signaller takes the recipient's response into account). We focused on the following factors: interactional context components (e.g., visual fields of both interactants), degree of use of signals ("rare" for signals performed by only a few subjects in the population or "common" for signals performed by many subjects), mechanical effectiveness, subjects' sociodemographic characteristics (e.g., age and hierarchy), and recipient species. We found a significant population-level right-hand bias for one type of human-directed gesture (SLAP HAND). Mechanical effectiveness influenced laterality: right-hand use was more pronounced for conspecific-directed gestures than for conspecific-directed manipulators. The laterality of conspecific-directed gestures overall did not differ from that of human-directed gestures. However, we found an indirect influence of recipient species on laterality as conspecific- and human-directed gestural lateralities were modulated differently by the position of the recipient in the signaller's visual field and by signaller's age. We hypothesize that the communication nature of gestures might have developed from manipulators. Manipulators may have contributed to the emergence and the evolution of the left-lateralized communication system in primates.

Keywords Gestural communication · Hemispheric lateralization · Language evolution · Manipulation · Motor effectiveness · Primate lateral asymmetry

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Introduction

Modern humans exhibit a strong right-hand preference at the population level for object manipulation (i.e., noncommunication actions) (e.g., McManus 1991) and gestural communication (e.g., Kimura 1973). Most studies of hand preference in young children have found that they use their right hand more for gestural communication than for object manipulation (bimanual coordinated and unimanual actions: e.g., Bates *et al.* 1986; Jacquet *et al.* 2012; Vauclair and Imbault 2009; see Fagard 2013 for a review). In contrast, observational, genetic, and functional neuroimaging studies reveal ambiguous relationships between the direction of brain lateralization for manipulation and for language (gesture and speech) in human adults (e.g., Badzakova-Trajkov *et al.* 2010; Cochet and Vauclair 2012; Knecht 2000; Häberling *et al.* 2016; Liu *et al.* 2009; Mazoyer *et al.* 2014; Tzourio-Mazoyer *et al.* 2015; see also McManus *et al.* 2013; Ocklenburg *et al.* 2013, 2014; Prieur *et al.* in 2018a for reviews). For instance, adult humans use their right hand more for bimanual coordinated actions (i.e., actions requiring manual role differentiation: Elliott and Connolly 1984) than for POINTING without speech (intentional signals are written in lower capitals) and the direction of laterality does not differ between bimanual coordinated actions and POINTING with speech (Cochet and Vauclair 2012). Together, these findings in infant and adult humans show that the nature of the relationship between the direction of handedness for manipulation and that for gestural communication is unclear. Further studies are needed to understand brain functional lateralization in manipulation and gestures. In particular, we need studies comparing manual asymmetries both within and between manipulation and signalling activities to gain a more complete understanding of different patterns of handedness, and of which characteristics are more strongly lateralized than others.

Comparative studies of manual laterality in our phylogenetically closest relatives, the nonhuman primates (hereafter primates), especially great apes, should help us better understand the nature of the relationship between human laterality for manipulation and language and the evolutionary roots of human right-handedness and language (e.g., Arbib *et al.* 2008; Corballis 2002; Meguerditchian *et al.* 2013; Prieur *et al.* 2018a; Versace and Vallortigara 2015). Several arguments support the view that gestural communication in our common primate ancestors played a key role in the emergence of human language. In particular, 1) primate gestural communication is particularly flexible in learning and use (e.g., Call and Tomasello 2007) resulting in large variation in the composition, morphology, and size of the gestural repertoire among individuals and groups of a given species; 2) the mirror system of the primate brain involved in the production and the perception of visuogestural actions and of orofacial communication is located in brain area F5, which is homologous to the language production area in humans (e.g., Fabbri-Destro and Rizzolatti 2008); and 3) the gestural communication system of primates shares several key characteristics with human language, such as intentionality (e.g., Call and Tomasello 2007) and referentiality (e.g., DIRECTED SCRATCHES: Pika and Mitani 2006). The body of evidence in favor of the evolutionary contribution of gestures to the emergence of human language has led researchers to hypothesize that gestural communication might be the precursor of the left-lateralized intentional communication system in primates (e.g., Gentilucci and Corballis 2006; Meguerditchian and Vauclair 2014). Here we restrict the term “gesture” to communication functions. We define a gesture as a movement of the limbs, head,

and/or body directed toward a recipient that is mechanically ineffective (i.e., “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 and de Waal 2007, p. 8185]) and receives a voluntary response from the recipient (e.g., Pika 2008; Pika and Bugnyar 2011; Prieur *et al.* 2016a). We distinguish gestures (such as TOUCH BODY) from “manipulators” (mechanically effective social actions used to get things done, such as GRAB BODY) which imply physical/forceful handling of a recipient to attain the desired goal without direct and voluntary involvement of the recipient. While gestures involve only communication components, manipulators involve both manipulation and communication components.

The majority of studies of primate laterality compare manual laterality between manipulation activities and gestures directed toward humans or toward both humans and conspecifics (pooled data) (e.g., chimpanzees, *Pan troglodytes*: Hopkins *et al.* 2005a; olive baboons, *Papio anubis*: Meguerditchian and Vauclair 2006). Overall, these studies show that primates use their right hand more for gestural communication than for manipulation actions directed toward objects (see Prieur *et al.* 2018a for a recent review). However, these studies consider relatively few gesture types: mostly FOOD BEG and POINTING (e.g., Hopkins *et al.* 2005a), and to a lesser extent HAND SLAP (Meguerditchian and Vauclair 2006, 2009), THROW OBJECT (Hopkins *et al.* 2005b) and species-typical gestures including THREAT, EXTEND ARM, and HAND SLAP (Meguerditchian *et al.* 2010). No study has yet compared manual laterality in manipulation actions and gestures in a purely conspecific context, although this has greater socioecological validity than human-directed communication (e.g., Marchant and McGrew 2013). Furthermore, no study has yet compared laterality in manual actions directed toward a social partner and gestures, although such comparisons would provide additional information concerning the evolutionary pathways by which gestures have emerged. It has been hypothesized that manual actions that are mechanically effective and devoid of a communication function evolved into manual imperative gestures (mechanical ineffective signals used to make the targeted recipient do something for the signaller, e.g., to obtain an object) in both phylogeny and ontogeny (e.g., Liebal and Call 2012; Scott and Pika 2012, cf. Pika and Fröhlich 2018 for the alternative Social Negotiation Hypothesis for the acquisition of gestural signalling). Within the framework of the evolutionary roots of human right-handedness and language, investigation of the effects of mechanical effectiveness on the laterality of manual intentional signals in our closest relatives can deepen our understanding of 1) the lateralized cerebral structures controlling manipulators and gestures performed in signalling contexts, and 2) the contribution of manual actions directed toward a social partner (so-called manipulators) to the emergence of the left-hemisphere specialization for communication activities (gestures and speech) in humans.

The theory of the evolution of laterality at the population level states that laterality has been shaped by intraspecific and interspecific interactions (e.g., Ghirlanda and Vallortigara 2004; Ghirlanda *et al.* 2009; Vallortigara and Rogers 2005). However, only three studies have investigated the effects of recipient type (conspecific- vs. human-directed communication) on manual laterality. They found no differences in hand preference between recipient types (chimpanzees for a category of species-typical gestures combining THREAT, EXTEND ARM, and HAND SLAP: Meguerditchian *et al.* 2010; olive baboons for HAND SLAP: Meguerditchian and Vauclair 2006;

Meguerditchian *et al.* 2011). Further investigations considering other gestures are needed to better understand the influence of recipient species on laterality.

Several factors modulate manual laterality in both human and other primates. These factors include characteristics of the contact target (e.g., inanimate: objects, ground, or enclosure; animate: conspecific or self), gestural characteristics (e.g., sensory modality: visual, auditory, or tactile; degree of use of signals in the population: “rare” for signals performed by only a few subjects in the population or “common” for signals performed by many subjects in the population), characteristics of the interactional context (e.g., visual field and body sides of signaller and recipient: left or right; emotional valence of the context: positive or negative), and sociodemographic characteristics of signallers and recipients (e.g., age, sex, and hierarchy) (e.g., Forrester *et al.* 2012, 2013; Prieur *et al.* 2016a, 2018b). For example, a recent study found that chimpanzees show a right-hand bias at the population level for the majority (13 of 21) of their most frequent conspecific-directed gestures (Prieur *et al.* 2016a). Chimpanzee signallers used their right hand overall more for common gestures than for rare gestures. Furthermore, chimpanzee signallers used their right hand more frequently for common gestures performed in negative/agonistic contexts than in positive/affiliative contexts. These findings show the importance of investigating manual laterality by taking several potentially influential factors and their mutual interactions into consideration simultaneously.

Here, we investigated the influence of mechanical effectiveness and recipient species on manual intentional signal laterality in chimpanzees, adopting a comprehensive approach. We addressed three questions and their associated hypotheses and predictions:

Question 1) Do chimpanzees show a right-hand bias at the population level for conspecific-directed manipulators (mechanically effective) and for frequently expressed human-directed gestures (mechanically ineffective)? To answer this question, we evaluated the direction of hand preference at the population level for each conspecific-directed manipulator and human-directed gesture separately. We formulated the following hypothesis and related prediction:

Hypothesis 1) Given that manipulators imply physical/forceful handling of a recipient, they should be more influenced by the (nonlateralized) environment than gestures. Furthermore, while gestures involve only communication components, manipulators involve both manipulation and communication components and these two components would interfere with each other affecting right-hand use.

Prediction 1) Chimpanzees will show a more pronounced right-hand bias at the population level for gestures than for manipulators.

Question 2) Does manual laterality differ between conspecific-directed manipulators and conspecific-directed gestures? We compared manual asymmetry in gestures and manipulators taking into account three categories of factors known to modulate gestural laterality (e.g., Prieur *et al.* 2016a): interactional context components (visual fields of both interactants and emotional valence of context), signal characteristics (degree of use of signal), and sociodemographic characteristics of the signaller and recipient (age, sex, group/zoo, position in the hierarchy, kinship, and dyadic affiliation). We formulated two hypotheses and related predictions:

Hypothesis 2a) The (nonlateralized) environment and the manipulation and communication components interfering with one another should affect right-hand use for manipulators.

Prediction 2a) Mechanical effectiveness would influence manual laterality, and that right-hand use should be greater for conspecific-directed gestures than for conspecific-directed manipulators (involving both manipulation and communication functions).

Hypothesis 2b) Laterality of manipulators is modulated by several factors as shown by our previous study for laterality of gestures in chimpanzees (Prieur *et al.* 2016a).

Prediction 2b) Signallers' manual laterality for manipulators and gestures would be modulated by interactional context components, degree of use of signal, and to a lesser extent, individual sociodemographic characteristics.

Question 3) Does manual laterality differ between human-directed gestures and conspecific-directed gestures? We evaluated manual laterality variability in relation to recipient type (conspecific or human) considering the influence of the same three categories of factors as for Question 2. We formulated the following hypothesis and related prediction:

Hypothesis 3) Chimpanzees adapt their communication strategy according to the interactional context (e.g., Liebal *et al.* 2004) and components of the interactional context (visual fields of both interactants and emotional valence of context) influence their gestural laterality (e.g., Prieur *et al.* 2016a).

Prediction 3) Gestural laterality of chimpanzees would be modulated differently by the interactional context in relation to recipient species. As for Question 2, based on our previous findings, we predicted that manual laterality of signallers would be modulated by interactional context components, degree of use of signal, and to a lesser extent, individual sociodemographic characteristics (prediction 2b).

Methods

Subjects

We observed 39 chimpanzees raised under good captive conditions in three zoos: Leipzig Zoo (Germany) ($N=16$), Zooparc de Beauval (France) ($N=14$) and La Palmyre (France) ($N=9$). Following previous studies of wild (Goodall 1986) and captive (Hopkins and Leavens 1998) chimpanzees, we defined age categories as follows: immature (0–7 years), adolescent (8–12 years), young adult (13–20 years), mature adult (21–35 years), and elderly adult (over 35 years). Our chimpanzee population (26 females and 13 males) included 8 immatures, 6 adolescents, 7 young adults, 11 mature adults, and 7 elders (mean age = 20.9 years; $SD = 2.14$). See Prieur (2015) for a detailed description of housing conditions.

Observational Procedures

J. Prieur collected the observational data between July and December 2013 at Leipzig Zoo (333 h), Zooparc de Beauval (198 h), and La Palmyre (174 h), yielding a total of 705 h of

observation. He collected data by continuously recording all occurrences of behaviors of interest expressed by all members of the group (Altmann 1974; Martin and Bateson 1994). This method optimizes data recording and does not overlook rarely expressed behaviors. J. Prieur collected data in real time using a stopwatch, a pencil and paper, and a powerful pair of binoculars if necessary. He made observations from above and as close as possible to the subjects. He recorded data only when subjects were clearly visible. He observed all subjects for as similar durations as possible. We did not videotape any of the observations, making interrater reliability tests impossible. However, we performed interreliability tests for the same procedures in a study of human gestural laterality (Prieur *et al.*, unpubl. data.), and found an excellent level of agreement (Landis and Koch 1977) between two observers, suggesting that the observational and coding procedures used in the present study are valid and reliable: for gesture type ($\kappa = 0.956$), handedness ($\kappa = 0.968$), position of recipient in signaller's visual field during interaction ($\kappa = 0.795$), and position of signaller in recipient's visual field during interaction ($\kappa = 0.869$). The variable "emotional context of interaction" had high measure of raw agreement (98.69%) but not high κ statistics value ($\kappa = 0.493$) because of the rarity of negative emotional context (negative interactions represented a very small proportion (3.26%) of the social interactions). As mentioned by other authors, despite high raw agreement, a low κ value can be an artifact of a low prevalence for a particular finding (e.g., Cicchetti and Feinstein 1990; Feinstein and Cicchetti 1990; Yen *et al.* 2013).

Data analyzed here included 22 frequent intentional signals (Table 1).

General Coding Procedure for Social Interactions

We considered only signals produced during dyadic interactions with (a) conspecifics or (b) humans (i.e., zookeepers and visitors) that were characterized by four key characteristics of intentional communication: 1) sensitivity to the recipient's attentional state, shown by adjustment of the signaller's communication in relation to the recipient's attention (e.g., emitting a visual signal only when the recipient is looking at the signaller); 2) waiting for a response as shown by the signaller pausing for ≥ 2 s while maintaining visual contact with the recipient; 3) the signaller's apparent satisfaction when the initial signal was successful, shown by the signaller ceasing communication; and 4) the signaller's goal persistence when the initial signal did not achieve its social goal, shown by repetition and/or elaboration (e.g., Bates *et al.* 1979; Bruner 1981; Fröhlich *et al.* 2016; Leavens and Hopkins 1998). We defined the subject that initiated a social interaction as the signaller and the target of this interaction as the recipient. For each dyadic interaction, we recorded 1) the type of signal (Table 1 and [Electronic Supplementary Material \[ESM\] Table SI](#); see later for the coding procedure associated with each type of signal) and the limb (hand or foot) (left/right) used by the signaller to communicate; 2) the interactional context of signal production with the relative positions of both subjects before and during the interaction and the emotional context of the interaction; and (3) the identity and role (signaller or recipient) of the subjects, as described in the text that follows.

Coding Procedure for Conspecific- and Human-Directed Gestures

We considered four gestures directed toward humans, the majority of which we recorded during feeding times. We included the following conspecific gestural data

Table 1 Repertoire and detailed description of intentional signals used by chimpanzees in 2013 in three zoos: Leipzig Zoo, Zooparc de Beauval, and La Palmyre

Intentional signal	Description	Reference(s)	Species	Study site(s)
Gesture (mechanically ineffective)				
CLAP HAND*	Subject strikes one open hand (usually the one in the upper position) against the other hand.	Nishida <i>et al.</i> (1999)	Chimpanzees (<i>Pan troglodytes schweinfurthii</i>)	Wild
SLAP FOOT*	Subject hits ground/wall/object with the sole or heel of one foot.	Pika <i>et al.</i> (2003)	Gorillas (<i>Gorilla gorilla</i>)	Captivity
SLAP HAND*	Subject hits ground/wall/object with the palm of one hand.	Pika <i>et al.</i> (2003)	Gorillas (<i>Gorilla gorilla</i>)	Captivity
EMBRACE	One arm of signaller is stretched and raised to about head level with palm facing downwards or placed lightly on the recipient's body.	Roth (1995)	Bonobos (<i>Pan paniscus</i>)	Captivity
EMBRACE HALF	Subject puts one arm around a conspecific while walking.	Nishida <i>et al.</i> (1999)	Chimpanzees (<i>Pan troglodytes schweinfurthii</i>)	Wild
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; partners are initially side by side and facing the same. Direction	de Waal (1988)	Bonobos (<i>Pan paniscus</i>)	Captivity
EMBRACE VENTRAL/DORSAL*	Both arms are opened and the partner is hugged ventro/dorsoventrally (leading arm recorded), with belly contact.	de Waal (1988)	Bonobos (<i>Pan paniscus</i>)	Captivity
HAND ON	Subject places the palm of one hand on the head of another subject and leaves it there >2 s.	Pika <i>et al.</i> (2003)	Gorillas (<i>Gorilla gorilla</i>)	Captivity
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.	Pollack and de Waal (2007)	Chimpanzees (<i>Pan troglodytes</i>) and bonobos (<i>Pan paniscus</i>)	Captivity
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.	Pollack and de Waal (2007)	Chimpanzees (<i>Pan troglodytes</i>) and bonobos (<i>Pan paniscus</i>)	Captivity
PUSH*	Subject applies gentle pressure against another subject with one hand or arm.	Pika <i>et al.</i> (2003)	Gorillas (<i>Gorilla gorilla</i>)	Captivity
TOUCH BODY*	Subject makes gentle and brief (<5 s) contact with the recipient's body (except genitals) with one hand or arm.	Pika <i>et al.</i> (2003)	Gorillas (<i>Gorilla gorilla</i>)	Captivity

Table 1 (continued)

Intentional signal	Description	Reference(s)	Species	Study site(s)
TOUCH GENITAL*	Subject applies gentle and brief (<5 s) contact with the recipient's genitals with the flat of one hand.	Pika <i>et al.</i> (2003)	Gorillas (<i>Gorilla gorilla</i>)	Captivity
SHAKE OBJECT*	Subject moves an object (e.g., branch) back and forth with quick jerky movements of one arm while the subject is sitting or standing.	Kano (1992, 1998)	Bonobos (<i>Pan paniscus</i>)	Wild
Manipulator (mechanically effective)	A mother holds her infant ventrally close to her body with one hand and/or one arm.	Nishida <i>et al.</i> (1999)	<i>Chimpanzees (Pan troglodytes schweinfurthii)</i>	Wild
GRAB BODY*	Subject grasps the recipient's body (except genitals and lip) with the whole hand, fingers are bent.	Pika <i>et al.</i> (2003)	Gorillas (<i>Gorilla gorilla</i>)	Captivity
GRAB GENITAL*	Subject grasps the recipient's genitals with the whole hand, fingers are bent.	Pika <i>et al.</i> (2003)	Gorillas (<i>Gorilla gorilla</i>)	Captivity
GRAB LIP*	Subject grasps the recipient's lip with the whole hand, fingers are bent.	Pika <i>et al.</i> (2003)	Gorillas (<i>Gorilla gorilla</i>)	Captivity

Gestures are grouped by sensory modality (3 auditory, 10 tactile, then 1 visual signals) and arranged by alphabetic order. Gestural repertoire and detailed descriptions of gestures were taken from a previous publication (Prieur *et al.* 2016a). Intentional signals marked with * are followed by descriptions inspired from the mentioned reference(s); they are labeled differently because precisions based on personal observations have been added. Signal data analyzed in the present study included three sets of data: 1) a new set of data for the four manipulators (mechanical effective social actions: GRAB GENITAL, GRAB LIP, GRAB BODY, and CRADLE) for these 39 subjects; 2) a new set of data for the four human-directed gestures (CLAP HAND, SLAP FOOT, SLAP HAND, and SHAKE OBJECT) for 35 of these 39 subjects. The physical forms/descriptions of these four gestures are the same whatever the recipient type (human or conspecific); 3) a set of data for the 14 conspecific-directed gestures expressed by the same 39 subjects and previously analysed (Prieur *et al.* 2016a) but included here in other statistical analyses

we have previously analyzed (Prieur 2015; Prieur *et al.* 2016a) to reanalyze them within the scope of the present study:

- Four gestures directed toward conspecifics for comparison with human-directed gestures: CLAP HAND, SLAP FOOT, SLAP HAND and SHAKE OBJECT
- Ten gestures directed toward conspecifics for comparison with conspecific-directed manipulators: EMBRACE, EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, EXTEND HAND, HAND ON, KICK, PUNCH, PUSH, AND TOUCH BODY

Following earlier definitions of gesture (e.g., Pika 2008; Pika and Bugnyar 2011; Prieur *et al.* 2016a), we classified signals as gestures (movements of the limbs or head and body) only if they met the following criteria: they (a) were used to initiate (not continue) a social interaction, (b) were directed toward a particular recipient, (c) were mechanically ineffective (e.g., Pollick and de Waal 2007), and (d) induced a voluntary response from recipients (recipients could choose the behavioral outcome in contrast to mechanical effective signals when they are physically manipulated). When a signal fulfilled criteria (a) and (b) but not criteria (c) and (d), but fulfilled the criteria for intentionality, we defined it as a “manipulator” (i.e., a mechanical effective social action). Because only two gestures involved a foot (i.e., SLAP FOOT and KICK), we use the term “hand” from now on instead of “limb.” We recorded the hand used to communicate during dyadic interactions only when both hands of the signaller were free and positioned symmetrically with respect to the body midline of the subject before the interaction, without any environmental factors that could potentially influence the use of one hand (e.g., being close to a wall/bush/tree) (e.g., Forrester *et al.* 2012).

We recorded data when a gesture was expressed either singly or in bouts (i.e., sequences of gestures) (e.g., Byrne and Byrne 1991; Marchant and McGrew 1991). For bouts, we recorded only the first gesture of the sequence, following Pika *et al.* (2003, 2005a). The following conditions must be satisfied to consider a single gesture or a bout terminated: the hand of the signaller returned to its initial position (Meguerditchian *et al.* 2010) or switched to another noncommunication activity (e.g., foraging) or an incident (e.g., stumble) that could influence the use of one hand occurred (e.g., Harrison and Nystrom 2010). A change in hand activity must last for >3 s (e.g., the signaller ceased to communicate by leaving the location to search for food for >3 s) before another gesture was recorded to ensure statistical independence of data (e.g., Hopkins and de Waal 1995).

All 39 chimpanzees performed conspecific-directed gestures sufficiently frequently for subsequent statistical analyses. However, only 35 of the chimpanzees expressed human-directed gestures: 8 immatures, 6 adolescents, 5 young adults, 11 mature adults, and 5 elders; 23 females and 12 males.

Coding Procedure for “Manipulators”

We observed and recorded manipulators directed toward conspecifics during daily activities using the same observational procedure as for gestures to compare them with our previously reported conspecific gestural data (Prieur 2015; Prieur *et al.* 2016a) that we reanalyzed in the present study. The four conspecific-directed manipulators only

involved the tactile sensory modality without use of an object. All 39 chimpanzees performed these behaviors sufficiently frequently for statistical analysis.

Characteristics of Intentional Signals

We classified intentional signals (i.e., gestures and manipulators) based on previous descriptions (e.g., Pika *et al.* 2003; Prieur *et al.* 2016a, Table I, ESM SI). We considered 14 gestures as visual ($N = 1$), auditory ($N = 3$), or tactile ($N = 10$) and four manipulators as tactile (for definitions of signal categories see Pika *et al.* 2003, 2005a). The effects of social pressures on human laterality (e.g., see Llaurens *et al.* 2009; Schaafsma *et al.* 2009 for reviews) led us to divide these 18 intentional signals into 2 categories according to their degree of use among group members as follows: we categorized 3 of the 14 gestures and 3 of the 4 manipulators, each performed by fewer than 14 subjects, as “rare” signals, defined as signals performed by only a minority of our 39 subjects and the other signals (11 gestures and one manipulator) performed by at least 25 subjects as “common” signals, defined as signals performed by a majority of the subjects (see Prieur 2015 for further details). We defined the intentional signal characteristics—sensory modality (auditory, visual, or tactile) and degree of use (rare or common) following a pilot study (Prieur 2015). We included all intentional signal characteristics in statistical analyses.

Characteristics of the Interactional Context of Intentional Signal Production

We recorded the relative positions—visual field used and body side exposed—of both individuals before (i.e., the last positions during the 2 s before an interaction) and during each dyadic interaction. Most social interactions can be anticipated by the observer via the expression of particular behaviors by the signaller, such as gazing at the recipient, gaze alternation, and movement toward the recipient. Following Baraud *et al.*' (2009) definition of “enlarged field,” we use the term “visual field used” to refer to the recipient’s location in the signaller’s visual field. The left visual field is from the direction of the signaller’s head (0°) to the signaller’s left side (180°). The right visual field is from 0° to 180° to the right of the signaller. We found significant positive correlations between the positions of subjects before and during an interaction (Prieur *et al.* 2016a) so we retained only two position variables for the present study: the position of the recipient in the signaller’s visual field and the position of the signaller in the recipient’s visual field. Cases when we could not record the orientation of the signaller or the recipient were very rare: 5 of the 5161 occurrences of interactions/intentional signals.

We divided the emotional contexts of interactions into two categories: positive and negative. For each interaction/intentional signal, we inferred the emotional context according to 1) the functional consequences of the signal during the interaction (i.e., the response of the recipient to the signal), and, if necessary; 2) the global social context in which the interaction occurred (positive valence: affiliative, food, nurse, play, ride and travel; negative valence: agonistic; see Pika *et al.* 2003; Pollick and de Waal 2007 for definitions); and 3) the signaller’s facial (e.g., Parr and Waller 2006) and vocal expressions (e.g., Crockford and Boesch 2005; Goodall 1986) and, to a lesser extent, its whole-body expressions (e.g., Van Hooff 1973) (ESM Table SII). We classified a

gesture as positive when it was, for instance, accompanied by a relaxed facial expression, a vocalization used only in affiliative contexts (e.g., “Aaa” grunt) and a global social context of an affiliative nature (e.g., feeding).

Sociodemographic Characteristics of the Subjects

In addition to the demographic characteristics of subjects (e.g., age and sex), we considered subjects’ genetic relatedness (kin) and social relationships (affiliation and hierarchy) (Prieur 2015; Prieur *et al.* 2016a).

Each zoo provided kinship and genetic information. We defined three categories of chimpanzee pairs according to a threshold coefficient of relatedness: 1) “Parent–infant” including mother–infant and father–infant pairs (coefficient of relatedness (r) = 0.50); 2) “Siblings” including full siblings (r = 0.50) and half-siblings (r = 0.25); and 3) “Unrelated” for pairs of genetically unrelated subjects (r < 0.125).

Following previous studies (Prieur *et al.* 2016a), we used a dyadic affiliation index (DAI) to evaluate relationship quality based on the relative frequency of affiliative and agonistic behaviors within the dyad. We selected the following six strictly affiliative gestures (gestures that are expressed only in positive contexts: in 8986 interactions) to quantify affiliation: EMBRACE, EMBRACE HALF, EMBRACE LATERAL, EMBRACE VENTRAL/DORSAL, EXTEND HAND, and TOUCH BODY. We analyzed all agonistic interactions recorded (4334). This index increases with affinity, from 0 for the absence of affinity. We considered three categories of dyadic affiliation: 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).

Based on previous studies (Langbein and Puppe 2004), we determined hierarchical dominance relationships using agonistic interactions (Pollick and de Waal 2007). We considered all recorded agonistic interactions (4334). Agonistic interaction data included the following intentional signals: PUNCH, HAND SLAP, HIT WITH BRANCH, and GRAB BODY. We organized these data into sociometric matrices and analyzed them using MatMan 1.1 (Noldus Information Technology, Wageningen, Netherlands) (de Vries 1995, 1998; de Vries *et al.* 2006). We assigned each of the subjects in each zoo a rank from 1 (the most dominant) to N (the most subordinate). We considered three categories of hierarchical rank: “Subordinate,” “Intermediate,” and “Dominant” (Beauval group: five subordinates, five intermediates, and four dominants; Leipzig group: five subordinates, five intermediates, and six dominants; Palmyre group: three subordinates, three intermediates, and three dominants).

Statistical Analyses

We performed all statistical analyses with R version 3.0.3 (R Development Core Team 2014). We set the level of significance at 0.05.

Descriptive Statistics of Laterality at the Individual and Population Levels To enable statistical analyses (binomial test), we used only data for intentional signals (human-directed gestures and conspecific-directed manipulators) that were produced by at least six subjects and at least six times by each subject (e.g., Prieur *et al.* 2016a), except CRADLE (considered for comparison with previous studies), for which only four

subjects satisfied this criterion. To assess individual-level bias for each signal, we used a binomial test on the numbers of responses performed by an individual with its left and right hands. We categorized a subject as lateralized when it presented a significant bias (i.e., binomial test: $P < 0.05$) and as nonlateralized when there was no bias (i.e., binomial test: $P \geq 0.05$). For each individual, we evaluated the direction of asymmetry by calculating an individual Handedness Index (HI) using the formula $HI = (R - L) / (R + L)$, where R and L represent the total number of right- and left-hand responses respectively. We estimated the strength of individual hand preference by the absolute value of HI (ABS_{HI}). This procedure is similar to that used by previous authors (e.g., Harris and Carlson 1993).

For each signal, we assessed population-level biases for lateralized and nonlateralized individuals using a binomial test. For signals for which at least six subjects were lateralized, we assessed population-level biases for right-handers and left-handers using a binomial test. Considering laterality as a continuum (e.g., McGrew and Marchant 1997) rather than dichotomously, we evaluated the bias in hand use at the population level using a one-sample two-sided Student's *t*-test on HI values of all individuals when the HI distribution was normal (Shapiro–Wilk normality test) and by performing a one-sample Wilcoxon signed rank test when the HI distribution was not normal.

Because sample size is suspected to influence laterality direction and strength (McGrew and Marchant 1997; Palmer 2002), we used a Spearman correlation test to investigate potential effects of the number of data points per individual on the direction and strength of laterality.

Generalized Linear Mixed Model Analysis of the Multiple Influential Factors

We evaluated the effects of several variables on laterality using generalized linear mixed models (GLMM) for binary data (logistic regression) with hand use as the dependent variable. Random variables were the signaller's and recipient's identity to account for pseudo-replication due to repeated observations (Waller *et al.* 2013).

We used two GLMMs to assess whether, and how mechanical effectiveness (Question 2, GLMM 1) and recipient species (Question 3, GLMM 2) influenced the laterality of signallers taking simultaneously into account other variables assumed to influence manual laterality in social interactive context: the interactional context, signal type, and sociodemographic characteristics of both interactants (see Table II for a descriptive summary of dependent, fixed, and random variables of each model). We compared right-hand use between categories, grouping particular intentional signals:

- 1) To study the effect of mechanical effectiveness (GLMM 1), we compared two categories that both involved only the tactile sensory modality without the use of an object: one category included the 10 conspecific-directed gestures (mechanically ineffective) and the second category included the 4 conspecific-directed manipulators (mechanically effective). This grouping of 10 conspecific-directed gestures that involved only the tactile sensory modality without the use of an object was based on previous results that

Table II Variables used in general linear mixed models (GLMMs) to study the effects of mechanical effectiveness (GLMM 1) and recipient species (GLMM 2) in chimpanzees; behavioral data collected in 2013 in three zoos: Leipzig Zoo, Zooparc de Beauval, and La Palmyre

	Name	Type
GLMM 1	Dependent variable	
	Hand use	Dichotomous (L/R)
	Fixed variables	
	Mechanical effectiveness	Dichotomous (Yes/No)
	Position of recipient in signaller's visual field during interaction (SVF)	Dichotomous (L/R)
	Position of signaller in recipient's visual field during interaction (RVF)	Dichotomous (L/R)
	Emotional context of interaction	Dichotomous (Negative/Positive)
	Signaller's sex	Dichotomous (F/M)
	Signaller's age	Ordinal (Immature/Adolescent/Young adult/Mature adult/Elder)
	Recipient's sex	Dichotomous (F/M)
	Recipient's age	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)
	Dyadic affiliation index (DAI)	Ordinal (Low/Medium/Strong)
	Degree of use of signal	Dichotomous (Rare/Common)
	Random variables	
	Signaller's identity	Nominal
	Recipient's identity	Nominal
GLMM 2	Dependent variable	
	Hand use	Dichotomous (L/R)
	Fixed variables	
	Recipient type	Dichotomous (Conspecific/Human being)
	SVF	Dichotomous (L/R)
	RVF	Dichotomous (L/R)
	Emotional context of interaction	Dichotomous (Negative/Positive)
	Signaller's sex	Dichotomous (F/M)
	Signaller's age	Ordinal (Immature/Adolescent/Young adult/Mature adult/Elder)
	Zoo	Nominal (Beauval/Leipzig/Palmyre)
Signaller's hierarchical rank	Ordinal (Dominant/Intermediate/Subordinate)	
Random variable		
Signaller's identity	Nominal	

L: left, R: right, F: female, M: male

showed that sensory modality and the use of an object while gesturing modulate the laterality of gestures (Prieur 2015; Prieur *et al.* 2016a).

- 2) To study the effect of recipient species (GLMM 2), we compared a category of conspecific-directed gestures and a category of human-directed gestures (both categories included the same four frequently expressed gestures: CLAP HAND, SLAP HAND, SLAP FOOT, and SHAKE OBJECT). We considered only results associated with interactions involving “Recipient type,” which is the focus variable. The other variables/interactions included in GLMM 2 are present to account for any possible effect of “Recipient type” on the dependent variable “Hand use.”

We used the GLMMs in an iterative process to determine the optimal model with the lowest Akaike information criterion (AIC), that is, the model that represents the best compromise between a limited number of variables and interactions and a good fit to the data. At the beginning of the iterative procedure, we included all the fixed variables and all their possible interactions in the model. We reduced the risk of false positives in our model selection procedure by 1) basing our model selection on a type II Wald χ^2 test, which is more conservative than the likelihood ratio test; 2) using very few iterations; and 3) using a large number of data points per variable (e.g., Forstmeier and Schielzeth 2011). We used the `glmer` function (`lme4` package [Bates *et al.* 2014]) for the GLMM analysis. To test the fit of the optimal model to the data, we visually checked for equivariance, independence, and normality of model residuals using the `plotresid` function (`RVAideMemoire` package [Hervé 2014]). We checked the results provided by the GLMM analyses for potential outliers in the estimate (difference between least square means [LSmeans]), the standard error of the difference, and the `z.ratio` (ratio of the estimate to its standard error) (GLMM 1: see Table IV; GLMM 2: see Table V). We tested the main effects of GLMM 1 and GLMM 2 with type II Wald χ^2 tests using the `Anova` function (`car` package [Fox and Weisberg 2011]). We computed LSmeans and associated adjusted probabilities of right-hand use using the `lsmeans` function (`lsmeans` package [Lenth 2014]). We performed post hoc multiple comparison tests using Tukey’s Honest Significant Difference test (from here, noted “Tukey test”) to prevent type I errors and we calculated differences between LSmeans (`lsmeans` package).

Data Availability The datasets generated during and/or analyzed during the current study are not publicly available because they are the subject of further studies, but are available from the corresponding author on reasonable request.

Ethical Note

This study was noninvasive and involved only observations of animals in their enclosures: the study chimpanzees were well habituated to human observation before data collection, essential requirements to minimize stress to animals (e.g., Fedigan 2010). No experimental permits or ethical approvals were required.

The authors declare that they have no conflict of interest.

Results

Manual Laterality of Conspecific-Directed Intentional Signals and Human-Directed Gestures at the Population Level

We recorded 5161 occurrences of intentional signals: 3506 occurrences of conspecific-directed manipulators (mechanically effective) by 39 chimpanzees and 1655 occurrences of human-directed gestures (mechanically ineffective) by 35 chimpanzees. After applying the statistical criterion required for binomial tests we retained 3440 occurrences of conspecific-directed manipulators and 1611 occurrences of human-directed gestures for analysis of manual laterality at the population level (see ESM Table SI for details).

The mean numbers of occurrences per individual were 93 for the 4 manipulator types (min = 6, max = 338; SD = 98), and 64 for the 4 human-directed gesture types (min = 8, max = 295; SD = 67).

For conspecific-directed manipulators, significantly more subjects were nonlateralized than lateralized for GRAB GENITAL and GRAB BODY (binomial test $P \leq 0.039$; ESM Table SI). The mean percentage of nonlateralized subjects for the four manipulators was 76% (min = 57%, max = 89%, SD = 13.9). For human-directed gestures, significantly more subjects were lateralized than nonlateralized for CLAP HAND (binomial test $P = 0.004$). The mean percentage of nonlateralized subjects for the four human-directed gestures was 45% (min = 0, max = 63%, SD = 30.19). We found no statistically significant difference between the numbers of right-handed and left-handed subjects for either conspecific-directed manipulators or human-directed gestures (binomial test $P > 0.07$; Table SI).

Considering laterality on a continuum, rather than dichotomously, we found no population-level bias for the direction of hand preference for any of the manipulators (one-sample two-sided *t*-test and one-sample Wilcoxon signed rank test: $P > 0.1$; Table SI), the mean HI was -0.02 (min = -0.24 , max = 0.19 ; SD = 0.19) and the mean ABSHI was 0.29 (min = 0.21 , max = 0.39 ; SD = 0.09). We found a significant right-hand bias at the population level for only one human-directed gesture: SLAP HAND (Wilcoxon signed rank test $P = 0.005$), the mean HI was -0.22 (min = -0.002 , max = 0.32 ; SD = 0.15) and the mean ABSHI was 0.56 (min = 0.42 , max = 0.88 ; SD = 0.21).

For conspecific-directed manipulators, we found no significant relationship between the number of data points per individual and HI values (Spearman correlation test: $P > 0.5$; ESM Table SIII), but we found a significant negative relationship between the number of data points per individual and ABSHI for GRAB BODY ($N = 37$, $r_s = -0.34$, $P = 0.038$). For human-directed gestures, we found no significant effects of the number of data points per individual on HI and ABSHI values for any gesture (Spearman correlation test: HI: $P > 0.2$; ABSHI: $P > 0.2$).

Factors Influencing Signal Laterality and their Interactions

We retained four conspecific-directed manipulators (3506 interactions) and four human-directed gestures (1655 interactions) for multifactorial analysis of manual laterality. Within the scope of the present study, we reanalyze conspecific gestural data previously reported (Prieur 2015; Prieur *et al.* 2016a): 10 conspecific-directed gestures to study the effect of mechanical effectiveness (GLMM 1, 11,345 interactions) and four conspecific-directed gestures to study the effect of recipient species (GLMM 2, 9523 interactions).

The analysis of deviance results corresponding to these two GLMMs (Table III) showed that laterality of intentional signals (conspecific- and human-directed gestures and conspecific-directed manipulators) was modulated differently in relation to three categories of factors: interactional context variables (signaller's visual field, recipient's visual field, and emotional context), signal characteristic variables (degree of use, mechanical effectiveness, recipient type), and social (position in the hierarchy, kinship, dyadic affiliation) and demographic (age) variables.

Laterality of Conspecific-Directed Manipulators vs. Conspecific-Directed Gestures: The Study of Mechanical Effectiveness (GLMM 1)

Influence of Mechanical Effectiveness Our results showed an influence of mechanical effectiveness on manual laterality in chimpanzees (Table IV). Signallers were more right-handed when performing gestures (mechanically ineffective) than manipulators (mechanically effective) when the recipient was in the signaller's right visual field (Tukey test: $P < 0.0001$; Fig. 1a) and when the signaller was in the recipient's left visual field ($P < 0.0001$; Fig. 1b), in negative emotional contexts ($P = 0.023$; Fig. 1c), when gestures were directed toward a low affiliative/nonclose partner ($P = 0.0004$; Fig. 1d), for rare gestures ($P = 0.0002$; Fig. 2), and when signallers were young adults ($P = 0.002$).

Influence of Other Factors on Laterality Signallers used their right hand more when the recipient was in their right visual field than in their left visual field during interactions involving manipulators and gestures (Tukey test: $P < 0.0001$; Fig. 1a). Signallers used their right hand more when they were in the recipient's left visual field than in their right visual field (Tukey test: $P < 0.0001$; Fig. 1b), in negative than in positive contexts ($P < 0.0001$; Fig. 1c) and when interacting with a low affiliative/nonclose partner than with a medium affiliative partner ($P = 0.048$; Fig. 1d) for gestures. We found no such differences for manipulators (Table IV). Signallers were also more right-handed when performing rare than common gestures (Tukey test: $P = 0.020$; Fig. 2). In contrast, signallers were more right-handed for common than for rare manipulators (Tukey test: $P = 0.003$).

Laterality of Conspecific- vs. Human-Directed Gestures: The Study of Recipient Species (GLMM 2)

Influence of Recipient Type Our results revealed no direct influence of recipient type on manual laterality in chimpanzees (Table V). We found no recipient type effect on right-hand use of signallers whatever the signaller's age class (Fig. 3a) or the location of the recipient in their visual field (Fig. 3b).

Influence of Age Class of Signallers Mature adult signallers were more right-handed than young adults for conspecific-directed gestures (Tukey test: $P = 0.002$; Fig. 3a). For human-directed gestures, mature adult signallers were more right-handed than young adults and elders (young adult: Tukey test: $P < 0.0001$; elder: $P = 0.031$) and immature and adolescent signallers were more right-handed than young adults (immature: $P = 0.007$; adolescent: $P < 0.0001$).

Table III Results of an analysis of deviance to examine the effects of mechanical effectiveness (GLMM 1) and recipient species (GLMM 2) on right-hand use in chimpanzees; behavioral data collected in 2013 in three zoos: Leipzig Zoo, Zooparc de Beauval, and La Palmyre

	Fixed terms and associated interactions	χ^2	df	<i>P</i>	
GLMM 1	Mechanical effectiveness	0.104	1	0.747	
	Degree of use of signal	0.093	1	0.761	
	Signaller's visual field during interaction (SVF)	4406.784	1	<2.2e-16	
	Recipient's visual field during interaction (RVF)	195.244	1	<2.2e-16	
	Signaller's age class	7.705	4	0.113	
	Signaller's hierarchical rank	3.193	2	0.203	
	Affiliation	4.899	2	0.086	
	Emotion	34.898	1	3.475e-09	
	Recipient's age class	5.767	4	0.217	
	Kinship	3.188	2	0.203	
	Mechanical effectiveness \times Degree of use of signal	20.491	1	5.991e-06	
	Mechanical effectiveness \times SVF	79.807	1	<2.2e-16	
	Mechanical effectiveness \times RVF	56.223	1	6.469e-14	
	Mechanical effectiveness \times Signaller's age class	8.294	4	0.081	
	Mechanical effectiveness \times Signaller's hierarchical rank	4.01	2	0.129	
	Mechanical effectiveness \times Affiliation	8.666	2	0.013	
	Mechanical effectiveness \times Emotion	5.636	1	0.018	
	GLMM 2	Gesture directed toward both conspecifics and humans	137.124	3	<2.2e-16
		Signaller's age class	22.049	4	0.0002
Signaller's sex		0.642	1	0.423	
Signaller's hierarchical rank		0.117	2	0.943	
Recipient type		0.425	1	0.515	
Emotion		7.269	1	0.007	
SVF		79.274	1	<2.2e-16	
Gesture directed toward both conspecifics and humans \times Signaller's age class		178.569	12	<2.2e-16	
Gesture directed toward both conspecifics and humans \times Signaller's sex		16.448	3	0.001	
Gesture directed toward both conspecifics and humans \times Signaller's hierarchical rank		79.686	6	4.148e-15	
Recipient type \times Signaller's age class		22.623	4	0.0002	
Signaller's hierarchical rank \times Emotion		4.32	2	0.115	
Gesture directed toward both conspecifics and humans \times SVF		12.931	3	0.005	
Recipient type \times SVF		5.016	1	0.025	

χ^2 : value of the type II Wald χ^2 , *df*: degrees of freedom, *P*: *P*-value of the type II Wald χ^2 . Significant results are in bold

Influence of the Position of the Recipient in the Signaller's Visual Field during an Interaction Signallers used their right hand more when the recipient was in their

Table IV Results of post hoc multiple comparisons tests 1 to study the effects of mechanical effectiveness (GLMM 1) in chimpanzees with hand use as the dependent variable; behavioral data collected in 2013 in three zoos: Leipzig Zoo, Zooparc de Beauval, and La Palmyre

GLMM 1		Mechanical effectiveness × Degree of use of signal					
Contrast			Estimate	SE	z,ratio	<i>P</i>	
No, rare	–	Yes, rare	0.789	0.192	4.099	0.0002	
No, rare	–	No, common	0.257	0.089	2.891	0.020	
Yes, rare	–	Yes, common	−0.426	0.122	−3.476	0.003	
No, common	–	Yes, common	0.106	0.135	0.783	0.862	
		Mechanical effectiveness × SVF					
Contrast			Estimate	SE	z,ratio	<i>P</i>	
No, R	–	Yes, R	0.904	0.159	5.681	<0.0001	
No, R	–	No, L	3.394	0.056	60.761	<0.0001	
Yes, R	–	Yes, L	2.481	0.086	28.797	<0.0001	
No, L	–	Yes, L	−0.009	0.154	−0.061	1.000	
		Mechanical effectiveness × RVF					
Contrast			Estimate	SE	z,ratio	<i>P</i>	
No, R	–	Yes, R	0.069	0.156	0.442	0.971	
No, R	–	No, L	−0.861	0.054	−15.810	<0.0001	
Yes, R	–	Yes, L	−0.105	0.085	−1.231	0.607	
No, L	–	Yes, L	0.825	0.157	5.250	<0.0001	
		Mechanical effectiveness × Affiliation					
Contrast			Estimate	SE	z,ratio	<i>P</i>	
No, strong	–	Yes, strong	0.463	0.168	2.756	0.065	
No, strong	–	No, low	−0.220	0.089	−2.468	0.134	
No, strong	–	No, medium	0.026	0.087	0.296	1.000	
Yes, strong	–	Yes, low	−0.028	0.124	−0.229	1.000	
Yes, strong	–	Yes, medium	−0.214	0.124	−1.732	0.510	
No, low	–	Yes, low	0.655	0.157	4.173	0.0004	
No, low	–	No, medium	0.246	0.086	2.868	0.048	
Yes, low	–	Yes, medium	−0.186	0.128	−1.446	0.699	
No, medium	–	Yes, medium	0.223	0.181	1.233	0.821	
		Mechanical effectiveness × Emotion					
Contrast			Estimate	SE	z,ratio	<i>P</i>	
No, N	–	Yes, N	0.762	0.268	2.842	0.023	
No, N	–	No, P	0.788	0.124	6.340	<0.0001	
Yes, N	–	Yes, P	0.159	0.236	0.674	0.907	
No, P	–	Yes, P	0.133	0.084	1.573	0.394	

L: left, R:right, SVF: position of recipient in signaller’s visual field during interaction, RVF: position of signaller in recipient’s visual field during interaction, P: positive, N: negative, estimate difference between LSmeans, SE: standard error of the difference, z.ratio: ratio of the estimate to its standard error, P: Tukey’s *P*-value. Significant results are in bold

right visual field than in their left visual field for human-directed gestures (Tukey test: *P* = 0.001; Fig. 3b).

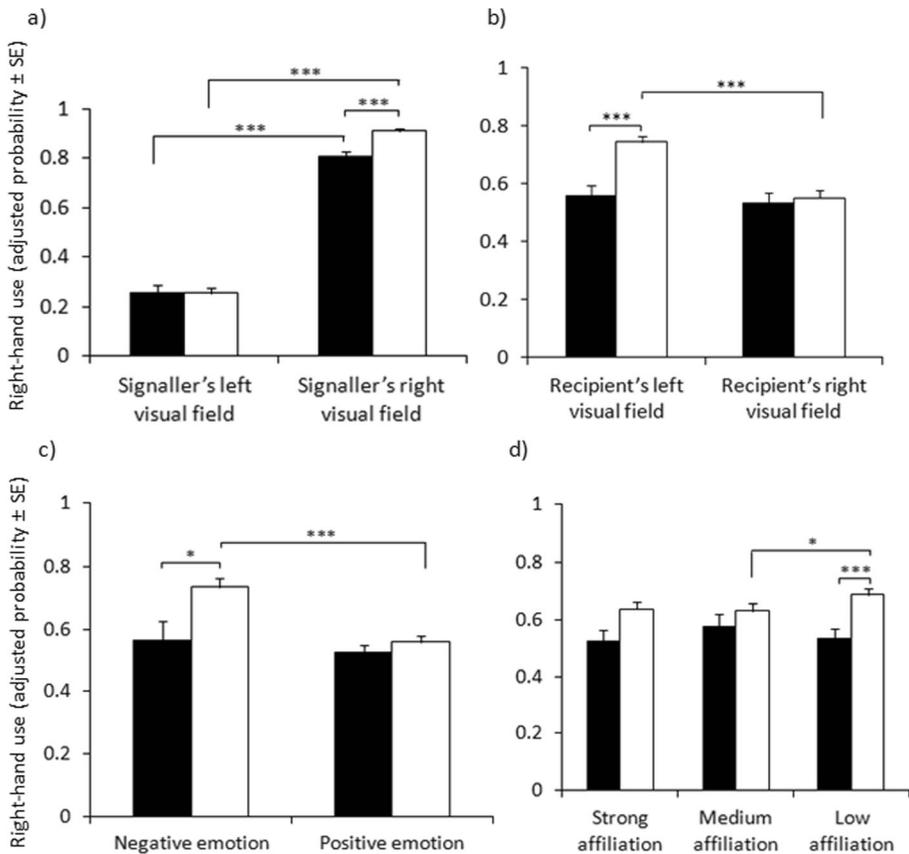


Fig. 1 Right-hand use for manipulators and gestures directed toward conspecifics (adjusted probability \pm SE) in chimpanzees; behavioral data collected in 2013 in three zoos: Leipzig Zoo, Zooparc de Beauval, and La Palmyre. **(a)** Interaction with signaller's visual fields: recipient in signaller's left or right visual field. **(b)** Interaction with recipient's visual fields: signaller in recipient's left or right visual field. **(c)** Interaction with emotional context. **(d)** Interaction with affiliation (GLMM 1). Black bars = conspecific-directed manipulators; open bars = conspecific-directed gestures. Tukey test: * $P < 0.05$; *** $P < 0.001$.

Discussion

Along the laterality continuum (e.g., McGrew and Marchant 1997), we found a significant right-hand bias at the population level for only one human-directed gesture (SLAP HAND) but not for manipulators. By comparison, our previous studies reported a right-hand bias at the population level for 6 of the 14 conspecific-directed gestures considered in the present study (see Prieur 2015; Prieur *et al.* 2016a for details). Here, we showed that mechanical effectiveness influenced manual laterality: manual laterality of signallers was overall more directed to the right for conspecific-directed gestures than for conspecific-directed manipulators. Moreover, laterality for conspecific-directed gestures and for human-directed gestures did not differ significantly. However, we found an indirect influence of recipient type on laterality: the location of the recipient in

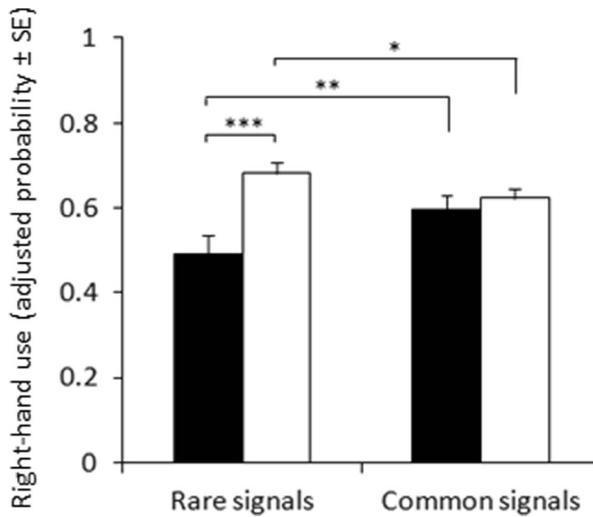


Fig. 2 Right-hand use for manipulators and gestures directed toward conspecifics (adjusted probability \pm SE) in chimpanzees; behavioral data collected in 2013 in three zoos: Leipzig Zoo, Zooparc de Beauval, and La Palmyre. Interaction with degree of use (GLMM 1). Black bars = conspecific-directed manipulators; open bars = conspecific-directed gestures. Tukey test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

the visual fields of signaller and the age class of signaller modulated laterality of human-directed gestures but not laterality of conspecific-directed gestures.

Manual Laterality of Conspecific-Directed Intentional Signals and Human-Directed Gestures at the Population Level

Considering laterality on a continuum, our results showed that only one type of human-directed gesture (SLAP HAND) elicited a right-hand bias at the population level but we found no hand bias for conspecific-directed manipulators. This result partly supports our hypothesis 1 and related prediction 1, that chimpanzees would show a right-hand bias at the population level for gestures but not for manipulators. However, previous studies revealed a population-level right-hand bias for conspecific-directed gestures (e.g., the majority of the most frequent conspecific-directed gestures of chimpanzees and gorillas: Prieur *et al.* 2016a, b) and for human-directed gestures (e.g., see Hopkins *et al.* 2012 for review). Compared to our previous studies in chimpanzees, proportionally more conspecific-directed gestures (6 of 14) presented a right-hand bias at the population level than did human-directed gestures (1 of 4). In particular, this was true when we considered only the four gestures common to both conspecific- and human-directed communication: three gestures (SLAP FOOT, SLAP HAND, and SHAKE OBJECT) were statistically right-lateralized at the population level when directed toward conspecifics whereas only SLAP HAND was statistically right-lateralized at the population level when directed toward humans. These findings reflect a similar population-level bias for SLAP HAND for olive baboons for both conspecific- and human-directed communication (Meguerditchian and Vauclair 2006; Meguerditchian *et al.* 2011). The difference in laterality between conspecific- and human-directed

Table V Results of post hoc multiple comparisons tests to study the effects of recipient species (GLMM 2) in chimpanzees with hand use as the dependent variable; behavioral data collected in 2013 in three zoos: Leipzig Zoo, Zooparc de Beauval, and La Palmyre

GLMM 2		Signaller's age class × Recipient type		Estimate	SE	z.ratio	<i>P</i>
Contrast							
Eld., conspecific	–	Ado., conspecific		–0.001	0.336	–0.004	1.000
Eld., conspecific	–	Imm., conspecific		–0.677	0.478	–1.415	0.923
Eld., conspecific	–	M.adu., conspecific		–0.498	0.403	–1.235	0.967
Eld., conspecific	–	Y.adu., conspecific		0.627	0.380	1.652	0.822
Eld., conspecific	–	Eld., human		0.525	0.238	2.203	0.455
Ado., conspecific	–	Imm., conspecific		–0.675	0.468	–1.444	0.913
Ado., conspecific	–	M.adu., conspecific		–0.497	0.281	–1.770	0.754
Ado., conspecific	–	Y.adu., conspecific		0.628	0.249	2.521	0.257
Ado., conspecific	–	Ado., human		–0.584	0.212	–2.758	0.151
Imm., conspecific	–	M.adu., conspecific		0.179	0.595	0.300	1.000
Imm., conspecific	–	Y.adu., conspecific		1.304	0.537	2.429	0.308
Imm., conspecific	–	Imm., human		–0.090	0.125	–0.720	0.999
M.adu., conspecific	–	Y.adu., conspecific		1.125	0.275	4.095	0.002
M.adu., conspecific	–	M.adu., human		–0.423	0.262	–1.618	0.840
Y.adu., conspecific	–	Y.adu., human		0.740	0.278	2.662	0.190
Eld., human	–	Ado., human		–1.110	0.398	–2.789	0.140
Eld., human	–	Imm., human		–1.291	0.499	–2.589	0.223
Eld., human	–	M.adu., human		–1.446	0.436	–3.314	0.031
Eld., human	–	Y.adu., human		0.842	0.430	1.961	0.627
Ado., human	–	Imm., human		–0.181	0.513	–0.353	1.000
Ado., human	–	M.adu., human		–0.336	0.342	–0.984	0.993
Ado., human	–	Y.adu., human		1.952	0.343	5.686	<0.0001
Imm., human	–	M.adu., human		–0.155	0.605	–0.256	1.000
Imm., human	–	Y.adu., human		2.134	0.567	3.765	0.007
M.adu., human	–	Y.adu., human		2.289	0.334	6.845	<0.0001
Recipient type × SVF							
Contrast				Estimate	SE	z.ratio	<i>P</i>
Conspecific, R	–	Human, R		–0.150	0.126	–1.186	0.636
Conspecific, R	–	Conspecific, L		0.224	0.100	2.237	0.114
Human, R	–	Human, L		0.591	0.160	3.691	0.001
Conspecific, L	–	Human, L		0.217	0.138	1.576	0.392

Imm.: immature, Ado.: adolescent, Y.adu.: young adult, M.adu.: mature adult, Eld.: elder, SVF: position of recipient in signaller's visual field during interaction, L: left, R: right, estimate difference between LSmeans, SE: standard error of the difference, z.ratio: ratio of the estimate to its standard error, *P*: Tukey's *P*-value. Significant results are in bold

gestures may be due to the interactional context and the use of communication strategy specific to the type of recipient.

Several studies report a left-hand bias for distinct actions directed toward conspecifics such as maternal cradling in various human cultures (e.g., Damerose

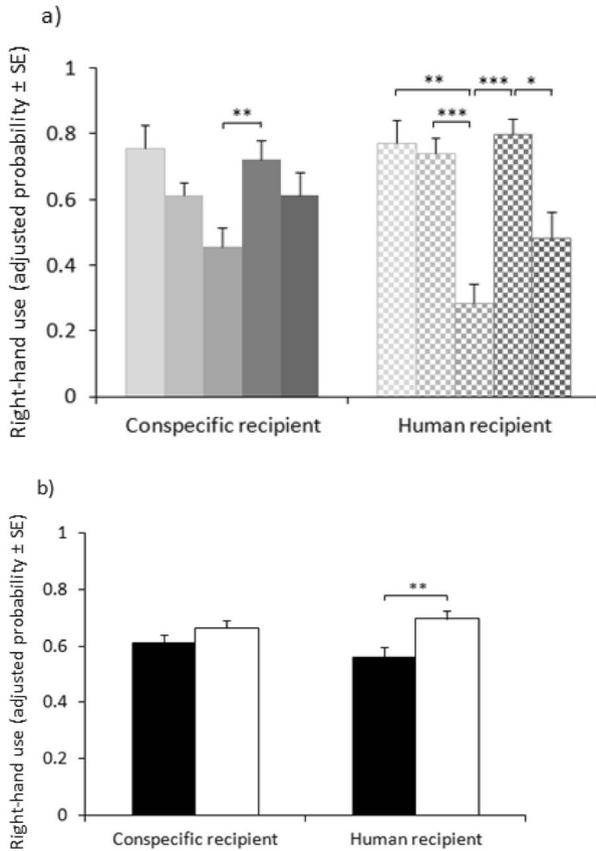


Fig. 3 Right-hand use for conspecific- and human-directed communication (adjusted probability \pm SE) in chimpanzees; behavioral data collected in 2013 in three zoos: Leipzig Zoo, Zooparc de Beauval, and La Palmyre. Interaction with **(a)** signaller's age class and **(b)** signaller's visual fields: recipient in signaller's left (SVF_L) or right (SVF_R) visual field (GLMM 2). Gradual range of gray = age classes from light gray (immature) to dark gray (elder); plain bars = conspecific-directed gestures; checkered bars = human-directed gestures; black bars = SVF_L; open bars = SVF_R. Tukey test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

and Vauclair 2002). In other primates, there is some evidence of a left-hand bias at the population level for CRADLE for great apes (e.g., Manning *et al.* 1994), but studies of Old and New World monkeys have yielded heterogeneous results (e.g., see Hopkins 2004 for review). We found no population-level bias for any of the conspecific-directed manipulators considered separately. Two nonexclusive reasons might explain the different lateralities between manipulators and gestures. First, laterality of manipulators would be more influenced by the (nonlateralized) environment than gestures. Second, as manipulators involve both manipulation and communication components, these components would interfere with each other, leading to the absence of a significant laterality bias. Therefore, our previous and present findings for chimpanzees support the hypothesis of a predominant implication of the left-cerebral hemisphere in the gestural communication system of primates (see Meguerditchian *et al.* 2013 for review).

Factors Influencing Signal Laterality and their Interactions

Laterality of Conspecific-Directed Manipulators and Conspecific-Directed Gestures: The Study of Mechanical Effectiveness (GLMM 1) We found a mechanical effectiveness effect on manual laterality: signallers overall used their right hand more for conspecific-directed tactile gestures than for conspecific-directed manipulators. These results support our hypotheses 2a and 2b and related predictions 2a and 2b concerning the effect of mechanical effectiveness on manual laterality: laterality of manipulators would be more environmentally/situationally constrained than gestures and laterality of manipulators (implying physical/forceful handling of a recipient) would be less governed by the communication component than would be laterality of gestures (involving only communication components).

Our findings are consistent with previous reports showing greater right-hand use for gestures than for object manipulations by human infants (e.g., Bates *et al.* 1986; Cochet *et al.* 2011) and several other primates (e.g., chimpanzees: Hopkins *et al.* 2005a; Meguerditchian *et al.* 2010; Prieur 2015; olive baboons: Meguerditchian and Vauclair 2006, 2009; red-capped mangabeys, *Cercocebus torquatus torquatus*, and Campbell's monkeys, *Cercopithecus campbelli campbelli*: Maille *et al.* 2013). Based on these findings, we hypothesize that components of communication and of manipulation (of both objects and conspecifics) do not share the same lateralized cerebral system in primates.

From a wider evolutionary perspective on the origins of gestures and left-hemispheric specialization in humans for manipulation and gestural communication, our findings are in line with the gestural communication literature proposing that gestures stem from manual actions deprived of a communication function (e.g., Liebal and Call 2012; Scott and Pika 2012). We hypothesize that the communication nature of gestures developed from manipulators (intentional actions involving both manipulation and communication functions). This may eventually have contributed to the emergence and the evolution of the left-lateralized system of intentional communication in primates. This system would have become increasingly lateralized and differentiated in the course of evolution to develop a specific left-hemisphere processing of gestures distinct from the cerebral system processing manipulation actions.

We found that other factors influenced laterality of chimpanzees. First, signallers were right-handed more when the recipient was in their right visual field than in their left visual field for conspecific-directed tactile gestures and conspecific-directed manipulators. One reason could be that signallers would be more likely to use their hand on the side where the recipient was (i.e., ipsilateral hand) to facilitate social interactions (Prieur *et al.* 2016a).

Second, signallers were right-handed more when they were in the recipient's left visual field than in their right visual field during an interaction involving conspecific-directed tactile gestures. We hypothesize that a more pronounced recipient's facial expression (via the left visual field: e.g., Wallez *et al.* 2012) enhances the emotional state of the signaller during an interaction and consequently increases right-hand use particularly in a negative emotional context (Prieur *et al.* 2016a).

Third, conspecific-directed tactile gestures were more right-lateralized in negative than in positive contexts. This effect of emotional context is supported by reports showing that negative emotional states (e.g., anger that frequently elicits approach motivation) in humans increased left-prefrontal brain activity inducing humans to use

their right hand in negative emotional contexts (see Rohlf and Ramirez 2006 for review). In contrast, we found that right-hand use for conspecific-directed manipulators was not influenced by emotional context. We hypothesize that laterality for manipulators (that involve a manipulation component) is less affected by the emotional component than gestural laterality, possibly because manipulators are less governed by communication components than are conspecific-directed tactile gestures.

Fourth, we showed that signallers were right handed more for common than for rare conspecific-directed manipulators. One explanation could be that common conspecific-directed intentional signals (i.e., signals performed by many subjects in our population) benefit by being more codified/lateralized than rare conspecific-directed intentional signals (i.e., signals performed by only a few subjects), resulting in potentially greater coordination that facilitates interactions. Ultimately, this facilitation would improve social cohesion. Our results concerning conspecific-directed tactile gestures are converse, showing that signallers were more right-handed for rare than for common gestures. However, this is congruent with our previous gestural findings in chimpanzees (Prieur 2015; Prieur *et al.* 2016a). This result could be further explained by the fact that 1) rare tactile gestures were performed mainly by subordinates (68%) contrary to common tactile gestures (44%) and 2) that subordinate chimpanzees overall used their right hand more to produce gestures than did higher ranking signallers (i.e., intermediate and dominant signallers) (Prieur 2015; Prieur *et al.* 2016a).

Fifth, signallers were right handed more for conspecific-directed tactile gestures toward a low affiliative/nonclose partner than toward a medium affiliative partner. Signallers interacted using tactile gestures in negative contexts more often with a low affiliative/nonclose partner (15.12% of tactile gestures) than with a medium (5.53%) or a strong (0.82%) affiliative partner (Prieur 2015). As mentioned earlier, negative emotions would induce greater right-hand use. This valence effect could thus explain that signallers were right-handed for conspecific-directed tactile gestures more when they were interacting with a low affiliative/nonclose partner than with a medium affiliative partner. However, we found no such valence effect when signallers were interacting with a strong affiliative partner, and this might be due to a counterbalancing effect: tactile interactions with a strong affiliative partner were engaged mainly (69.39%) by subordinate signallers that were particularly right handed (Prieur 2015). Concerning conspecific-directed manipulators, no evidence of an affiliation effect on signallers' right-hand use was found. One reason could be that conspecific-directed manipulators would be governed by communication components less than conspecific-directed gestures. Consequently, manipulators would be less affected by emotional context and psychosocial stress, contrary to gestures.

Laterality of Conspecific- and Human-Directed Gestures: The Study of Recipient Species (GLMM 2) We found no statistical differences in right-hand use between conspecific and human-directed gestures. This is in agreement with the literature (Meguerditchian and Vauclair 2006; Meguerditchian *et al.* 2010, 2011). Great apes mostly produce imperative gestures which are used to manipulate other group members to do something for them. Declarative gestures, which are used to direct the attention of others to an outside object or event (e.g., Liebal and Call 2012; Pika *et al.* 2005b), are produced less frequently. In the present study, chimpanzees mostly performed human-directed gestures toward zookeepers for imperative purposes, namely to obtain

something that they wanted (i.e., food items). One possible explanation for the absence of difference in hand preference between recipient species (conspecific or humans) might be that the four focus gestures common to both conspecific and human-directed gestures (i.e., CLAP HAND, SLAP FOOT, SLAP HAND, and SHAKE OBJECT) have the same function, namely, an imperative function one.

We found an indirect influence of recipient species on laterality as both conspecific- and human-directed gestural lateralities were modulated differently by the position of recipient in the visual field of signaller and the age of signaller. This result supports our hypothesis 3 and related prediction 3, as this difference between conspecific- and human-directed gestural lateralities may be due to the interactional context and the use of a communication strategy specific to the recipient type, as detailed later.

Signallers were right-handed more when the recipient was in their right visual field than in their left visual field for human-directed gestures but not for conspecific-directed gestures; this could be explained as follows. Three of the four gestures combined for GLMM 2 involved the auditory sensory modality (CLAP HAND, SLAP FOOT, and SLAP HAND) and one involved the visual sensory modality with use of communication tool (SHAKE OBJECT). We previously found that, chimpanzee signallers used their ipsilateral hand more than their contralateral hand to a conspecific recipient for tactile and visual gestures, possibly to facilitate transmission of these intentional signals (Prieur *et al.* 2016a). In contrast, signallers used their contralateral hand more than their ipsilateral hand to a conspecific recipient for auditory gestures, possibly to keep their ipsilateral hand free to be used for further potential tactile or visual gesture(s) toward the recipient (e.g., for a PUSH). However, this particular laterality pattern associated with auditory gestures was not the pattern observed here for the category combining the four gestures. The laterality pattern of the category combining the four gestures would have been affected by the inversed laterality pattern associated with the visual gesture SHAKE OBJECT.

Two complementary reasons could explain the difference of laterality patterns of human-directed gestures between the situations when the recipient was in the left or right visual field of the signaller. First, chimpanzees performed human-directed gestures mainly toward zookeepers to capture their attention when the latter fed them from a distance, throwing them various types of food items (*personal observations*). Our observations are in line with a recent report showing that chimpanzees are able to use distal gestural communication in interactions with a human experimenter about out-of-reach food (Leavens *et al.* 2015). Our chimpanzees produced human-directed gestures mainly in a unique and relatively positive social context contrary to conspecific-directed gestures performed in various social contexts including positive and negative contexts. Therefore, we hypothesize that laterality of chimpanzees for human- and conspecific- directed gestures may be influenced differently in relation to the socioecological context. This hypothesis is consistent with the literature in human and other primates showing that the environment context/setting (e.g., nature versus nonnature) may shape manual laterality (e.g., Marchant and McGrew 2013).

Second, interindividual distances were usually much greater for human-directed gestures than for conspecific-directed gestures and chimpanzees could never interact physically with humans contrary to conspecifics. To sum up, when chimpanzees are used to interacting with humans in a unique and relatively positive social context, in

addition to greater interindividual distances and conditions precluding physical interactions, they might adapt their communication strategy by using their ipsilateral hand more for auditory gestures (that also involve the visual modality). Chimpanzees might do so to enhance their chance to capture the attention of the human distributing food. This hypothesis is supported by studies showing that chimpanzees use auditory and/or visual communication tactics to achieve specific and immediate socio-communication goals such as to manipulate the attentional state of a recipient (e.g., Hostetter *et al.* 2001; Liebal *et al.* 2004; Tagliatalata *et al.* 2015).

We found no clear effect of age on right-hand use for either conspecific- or human-directed gestures. This absence of age effect on gestural laterality is in accordance with some previous findings (e.g., chimpanzees for THROWING directed toward both humans and conspecifics [pooled data]: Hopkins *et al.* 2005b) but the fact that others report an increase of right-hand preference with age (e.g., chimpanzees for human-directed FOOD BEG and POINTING [pooled data]: Hopkins and Leavens 1998) makes it difficult to draw firm conclusions about the influence of age.

Conclusions

We show first that our chimpanzees were right-handed at the population level for only one type of human-directed gesture (SLAP HAND) and found no hand bias for conspecific-directed manipulators. Second, we found that laterality of chimpanzees was influenced by the type of activity (conspecific- and human-directed gestures, conspecific-directed manipulators), also modulated differently in relation to three categories of factors: interactional context (visual fields of signaller and recipient as well as emotional context); degree of use of intentional signals; and, to a lesser extent, individual sociodemographic characteristics (age and affiliation). Based on our findings and the literature, we hypothesize that components of communication and of manipulation (of an object or a conspecific) do not share the same lateralized cerebral system in primates. Taking a wider evolutionary perspective on the origins of gestures and left-hemispheric specialization in humans for manipulation and gestural communication, we hypothesize that the communication nature of gestures might have developed from manipulators. Ultimately, the intentional communication system would have become increasingly lateralized and differentiated through evolution to elaborate a specific left-hemisphere processing of gestures distinct from the cerebral system processing manipulation actions.

Our findings concerning the effect of recipient species on gestural laterality support previous studies showing that laterality of conspecific-directed gestures does not statistically differ from laterality of human-directed gestures. However, we showed that recipient species influenced laterality indirectly: laterality of human- and conspecific-directed gestures was modulated differently by the location of the recipient in the visual fields of signaller and the age class of signaller. Our study highlights the need to investigate laterality using a comprehensive approach that takes into account different types of activity and as many potentially influential factors as possible to improve our understanding of the origins and evolution of human right-handedness and language.

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