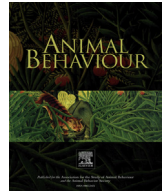




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Gestural development of chimpanzees in the wild: the impact of interactional experience

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To understand the complexity involved in animal signalling, studies have mainly focused on repertoire size and information conveyed in vocalizations of birds and nonhuman primates. However, recent studies on gestural abilities of nonhuman primates have shown that we also need a detailed understanding of other communicative modalities and underlying cognitive skills to grasp this phenomenon in detail. Here, we thus examined gestural signalling of chimpanzees, *Pan troglodytes*, living in two communities in the wild (Kanyawara, Uganda; Tai South, Côte d'Ivoire) with a special focus on the influence of the social environment on signal development. Specifically, we investigated to what extent specific social factors, namely behavioural context, interaction rates and maternal proximity, affect gestural production (i.e. gesture frequency, sequences and repertoire size). We used a combination of video recordings and focal scans obtained from 11 infants aged between 9 and 69 months during 1145 h of observation throughout two consecutive field periods. Overall, we found that social play was the context in which the highest number of gestures occurred. While gesture frequency and repertoire size increased with higher interaction rates with nonmaternal conspecifics and the number of previous interaction partners, no effect was found for interaction rates with mothers. Our results thus imply that infants of social mothers may have a head start in life. Moreover, we provide hitherto undocumented evidence for sex differences in gestural signalling, which may reflect the differential importance of early socialization for chimpanzee males and females. Gestural development thus relies heavily on interactional experiences with conspecifics, which adds support for gestural acquisition via the learning mechanism of 'social negotiation' in great apes.

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Communication systems vary greatly in the animal kingdom with respect to their degree of complexity, with human language representing one of the most sophisticated signalling systems (Hauser, Chomsky, & Fitch, 2002; Tomasello, 2008). Communicative complexity has been characterized in terms of the number of structurally and functionally distinct elements (e.g. repertoire sizes) or the number of information bits involved (Freeberg, Dunbar, & Ord, 2012). Studies have been strongly biased towards the vocal modality and have focused on repertoires, combinations (i.e. compositional syntax) and referential use as well as learning and modification of signals (for a review see Pollard & Blumstein,

2012). However, in recent years there has been a considerable increase of research interest concerning the production and use of multimodal and nonvocal signalling (Call & Tomasello, 2007; Liebal, Waller, Burrows, & Slocombe, 2013; Pika & Liebal, 2012), suggesting that communicative complexity should be interpreted and tested in relation to 'the number [usage and application] of capabilities that have to be coordinated' (after Oller & Griebel, 2008, p. 141).

Concerning gestural signalling, it has been well established that all great ape species use open-ended, multifaceted gestural repertoires, consisting of species-distinctive and species-indistinctive gestures (Call & Tomasello, 2007; Pika, 2015). Gestures are employed as intentional (e.g. Hobaiter & Byrne, 2011a; Leavens, Russell, & Hopkins, 2005; Pika, Liebal, Call, & Tomasello, 2005; Roberts, Roberts, & Vick, 2014) and flexibly produced

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communicative strategies, as demonstrated by means-ends dissociation and adjustments to audience effects (Call & Tomasello, 2007; Cartmill & Byrne, 2007), and may in some cases have a referential function (e.g. Douglas & Moscovice, 2015; Pika & Mitani, 2006). Moreover, evidence exists for the production of idiosyncratic and dyad-specific gesture types, implying that individual and social learning processes are involved in the acquisition of gestures (Fröhlich, Wittig, & Pika, 2016b; Halina, Rossano, & Tomasello, 2013; Pika et al., 2005; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994; but see Hobaiter & Byrne 2011a, 2011b for different views).

Research concerning different facets of communicative complexity and underlying cognitive mechanisms are thus crucial to grasp this phenomenon, if possible, in its full intricacy and develop a definition that is shared across species and communicative mediums. In addition, to understand the impact of ontogeny and socioecological factors, it is necessary to investigate the developmental trajectories of communicative signals. So far, it has been suggested that meaningful communicative signals develop first in interactions with the mother and are subsequently shaped in interactions with other members of the social community, such as siblings or peers (Maestripieri & Call, 1996; Plooij, 1978). However, although it has been shown that social experiences strongly influence sociocognitive outcomes (for reviews see Bard & Leavens, 2009; Leavens & Bard, 2011) and communicative development (Snowdon & Hausberger, 1997), this vital aspect has rarely been considered in studies of great ape communication (Bard & Leavens, 2014). The existing studies on gestural development have provided fine-grained analyses on a hitherto undocumented level, focusing on the onset, developmental trajectories and contextual usage of gestural signals (Bard et al., 2014; Halina et al., 2013; Schneider, Call, & Liebal, 2012a; Tomasello et al., 1997). However, they have all focused on individuals in captive settings and it is thus not clear to what extent these findings may be representative of the behaviour of individuals and groups living in their natural environments (Boesch, 2007; Fröhlich, Wittig, et al., 2016b). To gain an in-depth understanding of gestural signalling in great apes, it is important to study gestural ontogeny in populations living in their natural environment where they are exposed to active selection pressures (see also Boesch, 2007; Fröhlich, Kuchenbuch, et al., 2016). In addition, longitudinal approaches are useful tools to enable both between- and within-subject comparisons (Pika, Liebal, & Tomasello, 2003; Tomasello et al., 1994; Tomasello, Gust, & Frost, 1989) but they have only recently been implemented for great apes in the wild (Fröhlich, Kuchenbuch, et al., 2016; Fröhlich, Wittig, et al., 2016b).

The aim of the present study was thus to investigate whether specific factors related to social exposure, namely behavioural context, interactional experience and maternal proximity, affect the development of gestural signalling. To do so, we implemented a combination of methods using both high-quality video recordings and focal animal scans. Focal scan data of chimpanzee, *Pan troglodytes*, infants enabled us to trace both their social (e.g. interaction rates and partners) and their spatial independence (e.g. maternal proximity), which complemented the fine-grained analysis of communicative development. Therefore, we had the opportunity to examine multiple domains of development simultaneously. Systematic studies on the sociocomotor development in chimpanzees in their natural environments are extremely rare and have mainly focused on sex differences (Lonsdorf, Markham, et al., 2014) while the trajectory of physical development and maternal proximity has been neglected (however, see Koops, Furuichi, & Hashimoto, 2015 for a study addressing the influence of this factor on tool use). Given the large intersite variability in chimpanzee

social behaviour in the wild (Boesch, 2007; Boesch, Hohmann, & Marchant, 2002), we included two communities of different subspecies to obtain a more representative sample of the whole species.

Specifically, we observed the communicative, social and locomotor behaviour of six infants living in a community of eastern chimpanzees, *P. t. schweinfurthii*, in Kibale National Park, Uganda and five infants living in a community of western chimpanzees, *P. t. verus*, in Taï National Park, Côte d'Ivoire. We examined factors influencing signalling behaviour in three distinct contexts: food sharing, mother–infant joint travel and social play. These three contexts were chosen since they are known to involve frequent communicative exchanges (van Lawick-Goodall, 1967; Plooij, 1978; Wilkinson, Leudar, & Pika, 2012). To investigate social influences on gestural development, we analysed gesture frequency, gestural production in sequences and repertoire sizes as established measures of gestural signalling (Call & Tomasello, 2007; Hobaiter & Byrne, 2011a, 2011b). Specifically, we turned our attention to three research questions. First, does gestural signalling of infant chimpanzees differ in relation to behavioural contexts? To address this question, we investigated gestural production and repertoire produced in the three different contexts.

Second, is gestural signalling influenced by the interactional experience of a given infant? To answer this question, we linked focal scan data collected on social interactions with mothers and other conspecifics (e.g. grooming, play, affiliation) to data on gesture frequency, sequence and repertoire sizes. Importantly, interactions with mothers and interactions with other conspecifics were considered and analysed separately. Following the 'social negotiation hypothesis' (Fröhlich, Wittig, et al., 2016b), we assumed that developmental experiences and learning will play a major role in gesture acquisition and predicted that gesture production should be substantially enhanced by higher rates of social interaction with mothers and conspecifics.

Third, to what extent is gestural signalling of chimpanzee infants influenced by maternal proximity? To answer this question, we linked focal scan data collected on maternal proximity to data on gestural signalling. It has been argued that gestural ontogeny might depend crucially on the chimpanzee infant becoming spatially independent and leaving the security range provided by the mother (Van Lawick-Goodall, 1968). If this hypothesis is true, we predicted we would find an increase in gestural production in relation to an increase of physical distance between mother and maturing offspring (Bard et al., 2005). On the other hand, infants might feel more confident to practise and employ their first gestural signals with conspecifics while being in close proximity to their mother (Fröhlich, Wittig, & Pika, 2016a). With respect to this hypothesis, we predicted that the proximity of the mother would have a positive influence on gesture use.

In addition to age effects we also controlled for other confounding effects by including infant's sex, mother's parity and study site as factors in our analyses. We included the effect of sex since male and female chimpanzee infants might differ in gestural signalling resulting from differential roles of early socialization (Fröhlich, Wittig, et al., 2016a; Lonsdorf, Anderson, et al., 2014; Murray et al., 2014). Moreover, infants of multiparous mothers might have more social opportunities and interactions than infants of primiparous mothers (Fröhlich, Wittig, et al., 2016b; van Lawick-Goodall, 1967), especially if the latter immigrated relatively recently and only rarely associated with others. Finally, the substantial intersite variation reported for chimpanzee behaviour in the wild (Boesch et al., 2002) highlights the need to account for within-species variability in studies of communicative development.

METHODS

Study Sites and Subjects

The study was conducted with two different communities of chimpanzees: Kanyawara in Kibale National Park, Uganda, and Tai South in Tai National Park, Côte d'Ivoire. Detailed descriptions of the Kanyawara study area can be found in [Wrangham, Clark, and Isabirye-Basuta \(1992\)](#) and for Tai South in [Boesch and Boesch-Achermann \(2000\)](#). Observations were made on chimpanzees by M.F. during four periods between October 2012 and June 2014 (Kanyawara: March–May 2013; March–June 2014; Tai South: October–December 2012; October–December 2013). During the two study periods, the Kanyawara group varied between 53 and 56 individuals, and the Tai South community between 26 and 33 individuals. Chimpanzees were well habituated to human observers at both sites and have been studied regularly since 1987 at Kanyawara ([Wrangham et al., 1992](#)) and since 1994 at Tai South respectively ([Boesch & Boesch-Achermann, 2000](#)). It was therefore possible to observe most community members during dawn-to-dusk follows and to collect high-quality video and audio recordings of their social behaviour. In addition, at both sites we had access to long-term data on demography, social relationships and relatedness. We observed communicative interactions of 11 chimpanzee infants: Six infants were observed at the Kanyawara community and five at the Tai South community. Infant age ranged from 9 to 69 months (see [Table 1](#) for detailed information on subjects and data sets).

Data Collection

Observations of chimpanzee mother–infant dyads were carried out on average 5 days per week between 0700 and 1800 (dawn to dusk). We used an integrated focal-behavioural sampling approach ([Altmann, 1974](#)). Social interactions of infants (i.e. with both their mothers and other conspecifics) during the behavioural contexts of feeding, travel and play (for definitions of contexts see [Nishida, Kano, Goodall, McGrew, & Nakamura, 1999](#)) were recorded using a digital High-Definition camera (Canon Legria HF M41) with an externally attached unidirectional microphone (Sennheiser K6). The use of these devices enabled the collection of high-quality footage combined with observer comments and broad categories of vocalizations (continuous recording; [Martin & Bateson, 2007](#)). During a total of 1145 h of observation, we collected 189.6 h of video footage on the communicative behaviour of mother–infant dyads (Kanyawara: 93.5 h, mean \pm SD per infant = 15.6 \pm 6.7 h; Tai South: 96.1 h; mean \pm SD per infant = 19.2 \pm 4.1 h; see [Table 1](#)).

In addition, we conducted behavioural scans of all focal infants in 15 min intervals using a Pocket PC (HP iPAQ rx1959) (instantaneous sampling; [Martin & Bateson, 2007](#)). The following parameters for tracing of the motor and sociocognitive development of the infants and the maternal styles of mothers were collected: (1) behavioural context: feed, rest, solitary play, social play, groom, explore, travel, other (for definitions see [Nishida et al., 1999](#)); (2) interaction partner(s): ID of mother or other conspecific; (3) maternal proximity: body contact, within arm's reach, within 2 arm lengths, 1–2 m, 2–5 m, 5–10 m and >10 m (for further details on focal scan sampling see [Fröhlich et al., 2016b](#)).

This method resulted in 4519 scan sample points (Kanyawara: $N = 2301$, mean \pm SD per infant = 383.5 \pm 106.7; Tai South: $N = 2218$, mean \pm SD = 443.6 \pm 189.2; see [Table 1](#)). To investigate social and spatial independence in the present study, we used the rates of social interactions with mothers and with other conspecifics, the number of different interaction partners and maternal proximity (i.e. physical distance between infant and mother <2 m).

Coding Procedure

A total of 1120 high-quality recordings which contained clearly visible interactions in the investigated behavioural contexts (food sharing: $N = 260$; joint travel: $N = 392$; social play: $N = 468$) was available for coding using the program Adobe Premiere Pro CS4 v. 4.2.1 (Adobe Systems Inc., San Jose, CA, U.S.A.). Behavioural definitions were based on established ethograms of two long-term studies of eastern chimpanzees ([Goodall, 1986](#); [Nishida et al., 1999](#)) as well as several gesture studies conducted on chimpanzees in natural environments ([Fröhlich, Wittig, et al., 2016b](#); [Hobaiter & Byrne, 2011a](#); [Roberts et al., 2014](#)). Based on parameters used in previous work on great ape gesturing, a coding scheme was developed ([Pika et al., 2003, 2005](#)). While coding all agent-initiated interactions, we differentiated between food-sharing-, carry- and play-initiating behaviours via physical actions and intentionally produced gestures.

Gestures were defined as directed, mechanically ineffective movements of the body or body postures that elicited ('requested') a voluntary response by the recipient ([Pika, 2008](#)). We only considered intentionally produced gestures in our analyses that met one or more of the following key criteria of first-order intentionality ([Dennett, 1983](#)) established by research on human children and nonhuman primates ([Bates, Camaioni, & Volterra, 1975](#); [Bruner, 1981](#); [Leavens et al., 2005](#)): audience checking via eye gaze (signaller monitors the audience and visually orients towards the recipient before producing a signal); sensitivity to the recipient's attentional state (signaller adjusts to the recipient's

Table 1
Information on observed infants with respective observation time, recorded interaction time and scan sample points

Group	ID	Sex	Infant age P1 (months)	Infant age P2 (months)	Observation time (h)	Interaction time (h)	No. of focal scans
Kanyawara	WZ	M	9–11	21–23	105.5	17.7	417
	OB	M	13–15	25–27	119	23.0	458
	MM	F	13–15	25–27	87.5	8.6	360
	LL	F	N/A	15–17	60.5	8.0	252
	TR	F	16–18	28–30	112	23.0	532
	WC	M	55–57	67–69	73	13.2	282
Tai South	MH	F	10–12	22–24	150.5	17.7	572
	IN	M	N/A	10–12	91	14.0	373
	SL	M	15–17	27–29	148.5	22.9	556
	KY	F	19–21	31–33	157	23.8	576
	IT	M	64–66	N/A	41	17.7	141
Total	11	5:6	9	10	1145.5	189.6	4519

N/A: not applicable. The bottom line provides a summary for each column (P1/P2: first/second period of data collection).

state of attention, i.e. by using visual gestures only when in the recipient's visual field); and persistence to the goal (signaller waits for a response and modifies communicative behaviour if thwarted, e.g. by repeating/exaggerating the signal or by switching to a different modality; definitions based on Fröhlich et al., 2016b).

Gestures were clustered into three signal categories: audible (signals generate a sound while being performed, e.g. Slap Ground), tactile (signals include physical contact with the recipient, e.g. Touch) and visual (signals generate a mainly visual component, e.g. Raise Arm) signals (Pika et al., 2003). Gestural sequences included all cases where a gesture was produced in series, thus including both gestural bouts (separated by pauses of >1 s) and sequences (not separated by pauses of >1 s) as defined by Hobaiter and Byrne (2011b).

To assess the success of communicative attempts, we considered the behaviour of both the signaller and the recipient throughout the interaction, from the first requesting behaviour to the outcome, to assess whether a gesture reliably met the perceived goal (also termed 'goal-outcome match' or 'message-meaning overlap'; Cartmill & Byrne, 2010; Plooj, 1978; Smith, 1965). About 15% of coded interactions were coded for accuracy by a second observer and tested using the Cohen's kappa coefficient to ensure interobserver reliability (Altmann, 1974). A 'very good' level of agreement was found for gesture category ($\kappa = 0.815$) and gesture type ($\kappa = 0.853$), while a 'good' agreement was obtained for classification of intentional usage of gesture ($\kappa = 0.760$).

Statistical Analyses

We examined to what extent gestural signalling of infants was influenced by context, interactional experiences and maternal proximity while taking age, sex, mother's parity and site into account.

Response variables

To examine gestural production of chimpanzee infants, we used gesture frequency, gesture sequences and gestural repertoire size as the respective response variables in our three models. The first variable comprised gesture frequency based on the number of gestures per interaction. Second, gestural production in sequences was measured as number of gestures that were part of a sequence for each interaction. Necessarily, there might be some correlation with the variable of gesture frequency, but we still wanted to disentangle the aspect of serial gesture production from gesture production in general. For the third variable, we calculated the repertoire size as the number of gesture types used per individual. Note here that we do not use the term 'repertoire size' to refer to the complete gestural repertoire size per individual, as we included only three behavioural contexts of specific developmental stages of infants. Rather, we used this variable as a proxy for the communicative spectrum of individuals in a given month of life and make no claim that the numbers are complete.

Scan variables

The predictor variables were derived from focal scan sample points by calculating the mean of the presence/absence of the state/behaviour (interaction with nonmaternal conspecific, interaction with mother and maternal proximity) or the total number of individuals (number of previous interaction partners) during the 30 days before each communicative interaction. A minimal number of 32 sample points was used for calculations, corresponding to 8 h or a day of observation.

Model specification and implementation

To investigate the sources of variation in (1) gesture frequency, (2) gesture production in sequence and (3) gestural repertoire size, we used generalized linear mixed models (GLMMs; Baayen, 2008) with a Poisson error structure and log link function. In these models, we included context (three levels: food sharing, joint travel, social play; only models 1 and 2), interaction rates with maternal and nonmaternal conspecifics (continuous variables), number of previous interaction partners (range 1–14), maternal proximity (continuous variable) and age (in months; range 9–69) as our key test predictors. As control predictors in the model, we included sex (two levels: female, male), mother's parity (range 1–5) and study site (two levels: Kanyawara, Tai South). To test for interdependence of effects, we initially included the interaction terms between age and the scan variables related to interaction rates and partners. These interactions terms were excluded from further analyses if not significant. As random effects (intercepts) we included signaller, recipient and dyad identity in the model. To keep type 1 error rates at the nominal level of 5%, we also included the relevant random slopes components within signaller and recipient identity. Since sex and mother's parity did not vary within infants, for these variables we only included the random slopes within recipient identity (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009). We also did not include random slopes within dyad identity or correlations between random slopes and random intercepts to keep model complexity at an acceptable level and because neglected random slopes do not compromise type 1 error rates (Barr et al., 2013). In addition, we used 'log(hours of observation)' as an offset term and an observation level random effect, which models the extra-Poisson variation in the response variable using a random effect with a unique level for every data point (Gelman & Hill, 2006).

The models were implemented with the R statistical package (version 3.1.2; R Core Team, 2014) using the function `glmer` of the package `lme4` (D. Bates, Maechler, Bolker, & Walker, 2014). To test the overall significance of our key test predictors (Forstmeier & Schielzeth, 2011; Mundry, 2014), we compared the full model with a null model comprising only the control predictors and all random effects using a likelihood ratio test (LRT; Dobson, 2002). Prior to running the models we z-transformed the scan variables, age and parity (Aiken & West, 1991; Schielzeth, 2010). To control for collinearity we determined variance inflation factors (VIF; Field, 2005; Quinn & Keough, 2002) from a model including only the fixed main effects using the function `vif` of the R package `car`. This revealed collinearity generally not to be an issue (maximum VIF = 2.47). One exception was the variable 'maternal proximity', which had to be excluded from the third model (gestural repertoire size) owing to its strong collinearity with age (VIF = 5.63). Overdispersion appeared not to be an issue (dispersion parameters for gesture frequency: 0.55; gestures in sequence: 0.29; gestural repertoire size: 0.89). Tests of the individual fixed effects were derived using likelihood ratio tests (R function `drop1` with argument 'test' set to 'Chisq').

Ethical Note

Data collection was purely observational and noninvasive, with audio and video recordings taken from a minimum distance of 7 m, in an effort to avoid influencing the natural behaviour of the individuals, parties and communities. The research followed the recommendations of the 'Animals (Scientific Procedures) Act 1986', as published by the government of the United Kingdom, and the principles of 'Ethical Treatment of Non-Human Primates' as stated by the American Society of Primatologists. Approval for this study was gained from the Ministère de l'Enseignement Supérieur et de la

Recherche Scientifique (Côte d'Ivoire), the Office Ivoirien des Parcs et Réserves (OIPR; Côte d'Ivoire), the Uganda National Council for Science and Technology (UNCST; Uganda) and the Uganda Wildlife Authority (UWA; Uganda).

RESULTS

Overview of the Gestural Data Set and Repertoire

Overall, we identified 301 infant gesture cases in the food sharing, 77 in the joint travel and 688 cases in the play context, resulting in a total of 1066 gesture cases across contexts. On average, each infant contributed 96.9 ± 56.7 (mean \pm SD, Kanyawara = 88.8 ± 50.7 , Tai South = 106.6 ± 67.9) gesture cases to the data set. Of the total number, 566 cases were produced as part of a gesture sequence (food sharing: $N = 211$; joint travel: $N = 16$; play: $N = 339$). On average, infants produced 51.5 ± 37.3 (Kanyawara: $N = 42.7 \pm 27.4$; Tai South: $N = 62.0 \pm 47.8$) gestures as part of sequences.

We identified a total repertoire of 55 gesture types (Kanyawara: $N = 49$; Tai South: $N = 47$). Of these, seven were used exclusively in the food-sharing context, 37 solely in the play context and none exclusively in the joint travel context. Five types were used in all three contexts, four in both food sharing and play contexts and two in both joint travel and play. In other words, the play context comprised the majority of gesture types ($N = 48$), followed by the food-sharing ($N = 16$) and joint travel ($N = 7$) contexts. Infants used on average 25.1 ± 9.0 gesture types (Kanyawara: 27.8 ± 7.7 ; Tai South: $N = 21.8 \pm 10.2$). **Table 2** shows an overview of identified gesture types in relation to the categories and contexts used. Definitions of gesture types employed for food sharing are presented in **Appendix Table A1**. Definitions for gestures used to initiate joint travel are provided in **Fröhlich et al. (2016b)** and definitions for play solicitation gestures can be found in **Fröhlich et al. (2016a)**.

Significance of Key Test Predictors

To examine sources of variation in infants' gesture use, i.e. gesture frequency, the production of gestures in sequences and gestural repertoire size, we analysed effects of context, age, interaction rates with mothers and other conspecifics (included as two separate variables), number of interaction partners and maternal proximity, while taking sex, mother's parity and site into account. Overall, our key test predictors had a clear impact in all three models (LRT comparing the full with the null model for gesture frequency: $\chi^2_{10} = 30.015, P < 0.001, N = 610$; gesture production in sequences: $\chi^2_{10} = 30.008, P < 0.001, N = 610$; gestural repertoire size: $\chi^2_7 = 19.964, P = 0.006, N = 52$).

Influence of Behavioural Context

We found that gesture frequency was significantly lower in the joint travel context and higher in the play context than in the food sharing context (i.e. the reference category; **Fig. 1, Table 3**). In addition, significantly fewer gestures were used in sequences in the context of joint travel than for food sharing (**Table 3**).

Influence of Interactional Experience

Regarding gesture frequency, we found a significant interaction between age and the previous interaction rates with (nonmaternal) conspecifics: with increasing age, interaction rates with social partners other than the mother had a positive influence (**Fig. 2, Table 3**). For gestures produced in sequences, we found an

Table 2

Gesture types ($N = 55$) used by chimpanzee infants at Kanyawara and Tai South with regard to signal category and behavioural outcome

Gesture type	Category	Food sharing	Joint travel	Social play
Arm on	T		X	X
Bite	T	X		X
Bite pretend	V			X
Bob	V			X
Drum on	T			X
Embrace	T			X
Extend body size	V			X
Finger in mouth	T	X		X
Flail arm	V			X
Grab	T	X		X
Grab foot	T			X
Grab pretend	V	X		
Grab-push	T			X
Hand bent	V	X		
Hang sloth	V			X
Head butt	T			X
Hit	T			X
Hit with object	T			X
Hold object in mouth	V			X
Hold onto	T	X	X	X
Hover	V	X		
Kick	T			X
Lie down	V			X
Lie spread legs	V			X
Look	V	X	X	X
Look back	V		X	X
Look through thighs	V			X
Mouth beg	T	X		
Mouth stroke	T	X		
Palm-up	T	X		
Peer	V	X		
Poke	T			X
Present leg	V			X
Pull	T	X	X	X
Pull object	T			X
Push	T			X
Raise arm	V			X
Raise forearm	V			X
Reach	V	X	X	X
Rock	V			X
Rub genitals	T			X
Shake branch	AV			X
Slap ground	A			X
Somersault	V			X
Stiff walk	V			X
Steal object	T			X
Step on	T			X
Stomp	A			X
Swing	AV			X
Swing object	V			X
Tickle	T			X
Tilt head	V			X
Touch, long	T	X		X
Touch, short	T	X	X	X
Wrap arms	T			X
Total	55	16	7	48

(A: audible; T: tactile; V: visual; AV: audiovisual). The bottom line presents the sum of gesture types recorded for each context.

interaction between age and the number of previous interaction partners: with increasing age, the number of social partners had a positive influence on the number of gestures used in sequence per interaction (**Table 3**). By contrast, we found that neither of the three gesture parameters (i.e. frequency, production in sequences, repertoire size) was affected by previous interaction rates with the mother (**Fig. 3; Table 3**). However, gestural repertoire sizes increased with the number of previous interaction partners (**Fig. 4, Table 3**).

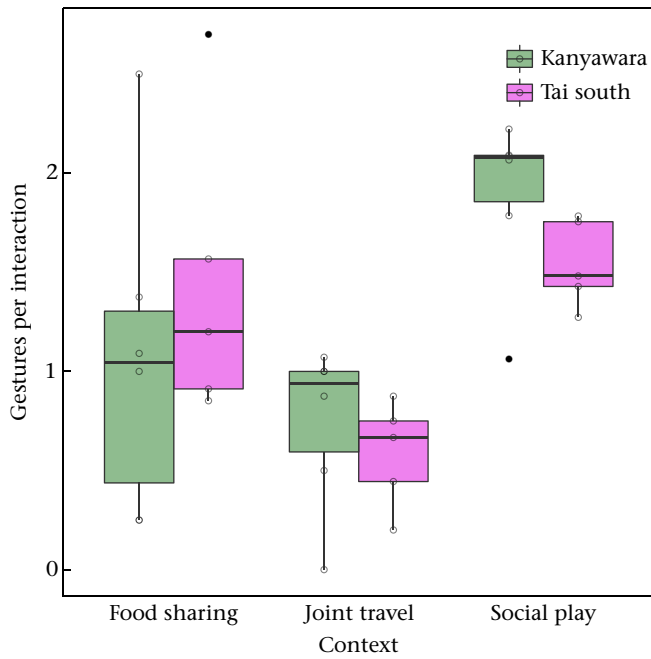


Figure 1. Influence of behavioural context on gesture frequency of infants at Kanyawara ($N = 6$) and Tai South ($N = 5$). Indicated are mean numbers per infant (open circles), median (horizontal lines), quartiles (boxes), percentiles (2.5 and 97.5%, vertical lines) and outliers (dots).

Influence of Maternal Proximity

There was no effect of maternal proximity on either gesture frequency or gestures produced in sequence (Table 3). With respect to gestural repertoire size (model 3), we were not able to test for the effect of maternal proximity owing to high collinearity with age ($VIF = 5.63$).

Influence of Sex, Mother's Parity and Study Site

While we only found a weak effect of sex on gesture frequency, and no effect on gesture production in sequences, male infants had a significantly larger gestural repertoire than females (Fig. 5, Table 3). Mother's parity had no significant effect on either gesture frequency, gesture sequence or gestural repertoire size (Table 3). In addition, gesture rates were on average higher, gestures more often used in sequences and gestural repertoire sizes larger in the Kanyawara infants than the infants from Tai South.

DISCUSSION

The present study aimed to examine whether specific factors, namely behavioural context, interactional experience and maternal proximity, influence gestural production and development. To do so, we studied the behaviour of chimpanzee infants living in two communities of different subspecies in their natural environments, taking potential within-species variability into account. To trace the gestural development of infants, we focused on three distinct parameters: gesture rate, gestural sequences and gestural repertoire size. Specifically, we had three objectives. First, we examined gestural production and repertoire size of chimpanzee infants with respect to three specific communicative behavioural contexts: food sharing, mother–infant joint travel and social play. Second, we investigated whether the interactional experience gained with mothers on the one hand and with conspecifics on the other

Table 3

Effects of behavioural context, interactional experience, maternal proximity and confounding variables (age, sex, mother's parity and study site) on gestural frequency, production in sequences and repertoire size derived using GLMMs with a Poisson error structure and log link function

	Estimate	SE	χ^2	P
Frequency				
Intercept	-3.911	0.153	NI	NI
Context [joint travel]	-0.676	0.23	7.237	0.007
Context [play]	0.335	0.106	9.756	0.002
Age	0.3	0.12	NI	NI
Interaction rate/nonmaternal	0.03	0.059	NI	NI
Interaction rate/maternal	-0.096	0.06	2.504	0.114
No. of interaction partners	0.015	0.058	0.069	0.793
Maternal proximity	0.187	0.12	2.426	0.119
Sex [male]	0.195	0.102	3.626	0.057
Mother's parity	0.025	0.054	0.218	0.641
Site [Tai]	-0.534	0.132	11.793	0.001
Age: interaction rate/nonmaternal	0.128	0.058	4.932	0.026
Production in sequence				
Intercept	-4.735	0.286	NI	NI
Context [joint travel]	-1.938	0.381	19.722	<0.001
Context [play]	-0.027	0.189	0.021	0.886
Age	0.607	0.277	NI	NI
Interaction rate/nonmaternal	-0.181	0.099	3.367	0.067
Interaction rate/maternal	0.06	0.107	0.321	0.571
Number interaction partners	0.085	0.107	NI	NI
Maternal proximity	0.3	0.226	1.770	0.183
Sex [male]	0.139	0.195	0.508	0.476
Mother's parity	0.101	0.103	0.958	0.328
Site [Tai]	-0.588	0.247	5.648	0.017
Age: no. of interaction partners	0.333	0.17	3.845	0.050
Repertoire size				
Intercept	-1.990	0.122	NI	NI
Age	0.155	0.066	4.209	0.040
Interaction rate/nonmaternal	0.028	0.075	0.138	0.710
Interaction rate/maternal	-0.018	0.073	0.061	0.805
No. of interaction partners	0.231	0.070	8.881	0.003
Sex [male]	0.342	0.133	6.465	0.011
Mother's parity	0.000	0.070	0.000	0.997
Site [Tai]	-0.293	0.136	4.031	0.045

Bold values indicate $P \leq 0.05$. NI: significance test not indicated because it has no meaningful interpretation.

affected gestural signalling. Third, we examined to what extent infants' gestural signalling was influenced by maternal proximity. In doing so, we controlled for potentially confounding effects of age, infant's sex, mother's parity and study site. Overall, we found that the majority of gestural signals and types were employed in the behavioural context of social play. Depending on infant age, interactional experience with nonmaternal conspecifics and the number of previous interaction partners were strong predictors of gesture frequency, gesture production in sequences and gestural repertoire size. In contrast, maternal proximity did not seem to affect infants' gestural signalling. Below, we discuss the results for each research question in detail.

Behavioural Contexts

We confirmed previous work suggesting that social play comprised the context within which gestures are most likely to be produced in great apes (Liebal, Pika, & Tomasello, 2006; Pika et al., 2003; Tomasello et al., 1997). Play interactions, especially between peers (see below), may serve as a context for experimentation, allowing individuals to test, shape and train their gestural usage, and gain experience that will be vitally important in adulthood (van Lawick-Goodall, 1967). Similarly, Lonsdorf, Andersson et al. (2014), Lonsdorf, Markham et al. (2014) highlighted the role of play in chimpanzee infancy in individuals living at the Gombe community, Tanzania, showing that solitary and social play comprise about a third of an infant's observation time at particular developmental

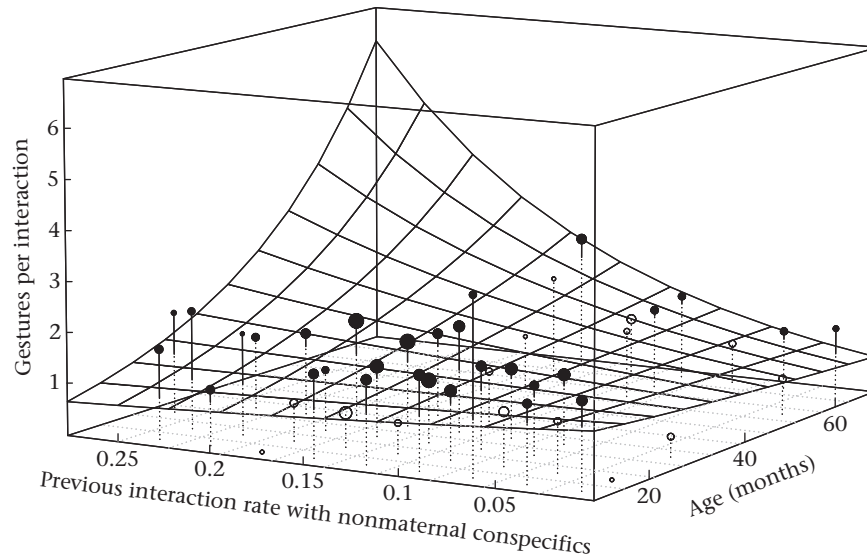


Figure 2. Influence of age and interactions with nonmaternal conspecifics on the gesture frequency of infants. The surface represents results from the GLMM with all covariates centred to a mean of zero; the points depict the average gesture frequency per cell of the surface. Values above the fitted model are depicted as filled points, values below as open points. The volume of the points corresponds to number of samples per cell.

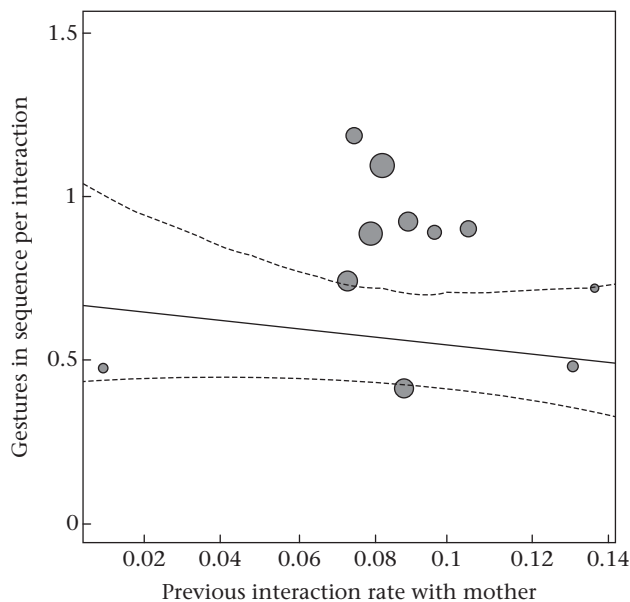


Figure 3. Influence of previous interactions with the mother on the infants' production of gestures in sequences. Depicted are mean numbers of gestures produced in sequences, separately for each infant against the mean interaction rate with its mother. The area of the dots corresponds to the sample size per individual (range 17–113); the solid and dashed lines represent the fitted GLMM and confidence interval based on all other covariates and factors centred to a mean of zero.

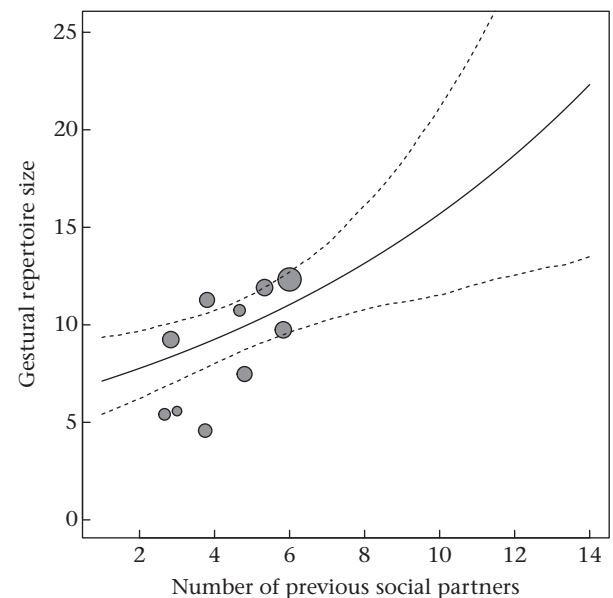


Figure 4. Influence of the number of interaction partners on infants' gestural repertoire size. Depicted are mean numbers of gesture types observed per month, separately for each infant against the mean number of previous interaction partners. The area of the dots corresponds to the sample size per individual (range 2–6); the solid and dashed lines represent the fitted GLMM and confidence interval based on all other covariates and factors centred to a mean of zero.

stages. Our results concerning gestural production and repertoire size to solicit food sharing indicate that this context also seems to play a role for gestural production and development in young apes, corroborating previous work of Bard (1992) on young free-ranging Bornean orang-utans, *Pongo pygmaeus*, in the Tanjung Puting Reserve, Indonesia. The repertoires of gestures and behaviours requesting food transfers might therefore be considerably larger than previously recognized (e.g. Gilby, 2006; Nissen & Crawford, 1936; Silk, Brosnan, Henrich, Lambeth, & Shapiro, 2013). In line with this premise, a recent study at the Ngogo chimpanzee community in Uganda described a comprehensive set of signals used to

request meat sharing (Wilkinson et al., 2012). What makes these signals particularly interesting is that these interactions qualify as 'triadic', that is they include a signaller, a recipient and a third entity (i.e. an external object; Bard, 1992; Liebal et al., 2006; Pika & Mitani, 2009; Tomasello et al., 1994). Moreover, previous studies have proposed a vital role of gestural signals in the context of tool use for food acquisition (nut cracking; Inoue-Nakamura & Matsuzawa, 1997). The feeding context may thus be useful for examining the role of triadic and referential gestural interactions in great apes. While systematic, quantitative studies of gestures used to elicit food sharing are still nonexistent (however, see Rossano & Liebal,

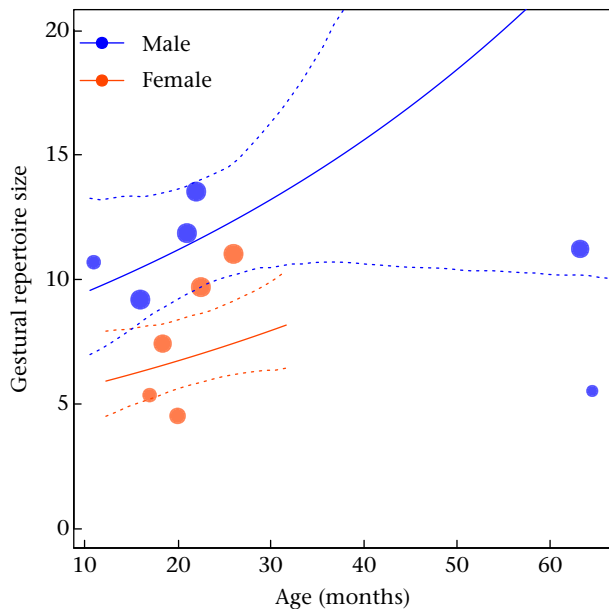


Figure 5. Influence of sex and age on infants' gestural repertoire size. Depicted are mean numbers of gesture types observed per month, separately for each individual against its mean age. The area of the dots corresponds to the sample size per individual (range 2–6); the solid and dashed lines represent the fitted GLMM and confidence interval based on all other covariates and factors centred to a mean of zero.

2014; Wilkinson et al., 2012 for application of conversational analysis to capture gestural interactions), they may comprise an important and fruitful avenue of research.

The context of mother–infant joint travel, in contrast, revealed the lowest number of gesture types and rates as well as the fewest gestures produced as part of sequences. In a recent study of this behavioural context, Fröhlich et al. (2016b) argued that the low frequency of gesturing and the different signal repertoires of infants compared to mothers were the result of high maternal initiation rates in natural environments coupled with diverging roles in these interactions. However, a study on bonobo, *Pan paniscus*, mother–infant joint travel in captivity found that infants solicited joint travel more often and produced a larger variety of gestures (Halina et al., 2013). Fröhlich et al. (2016b) speculated that these contrasting results may be consequences of potential interspecies differences in maternal styles and/or the distinct socioecological environments.

Interactional Experience outside the Mother–Infant Dyad

Regarding interactional experiences with conspecifics outside the mother–infant bond, we found a marked positive effect on the occurrence of gestural sequences and repertoire size depending on infant age. This result corroborates the prediction that social experience and context crucially impact upon communication skills. The social environment of nonhuman primates plays a vital role in the development of an individual's communicative abilities, with impaired socialization often directly resulting in the malfunction or lack of social responses in adulthood (Bard & Gardner, 1996; van Leeuwen, Mulenga & Chidester, 2014; Mason, 1963). Hence, communicative abilities rely on a combination of social, physical and cognitive development in the individual while interacting with the social and physical world surrounding it (Adamson, 1996; Bates, Benigni, Bretherton, Camaioni, & Volterra, 1979; Morisset, Barnard, Greenberg, Booth, & Spieker, 1990). Our findings suggest that the development of intentional gesturing in

chimpanzee infants depends on the opportunities they have to interact with conspecifics (Fröhlich, Wittig, et al., 2016b; Plooij, 1978). While the mother–infant relationship is critical for normal social development (Maestripieri, 2009), research also demonstrates that early socialization in the wider social environment is essential to develop social competency later in life (Hamilton, 2010; Parker & Asher, 1987). In the fission–fusion social structure characteristic of chimpanzees (Aureli et al., 2008), the mother can actively influence her offspring's social environment through selective subgrouping (Murray et al., 2014). Even from a very early age, chimpanzees seem to exploit these social opportunities, with the number of social partners increasing with offspring age and distance to the mother (Lonsdorf, Markham, et al., 2014; Murray et al., 2014). In light of the importance of social bonds and master–apprentice relationships in chimpanzee society (Matsuzawa et al., 2001), such a strategy appears to be crucial for a chimpanzee to become a high-ranking member of the community and secure future access to food resources, stable growth and reproductive success (Mitani, 2009; Muller & Mitani, 2005).

For vocal development in birds and mammals it has also been suggested that, in contrast to imitation, experiences in social interactions (e.g. responses of conspecifics) play a substantial role through the introduction of new sounds and encouragement of improvisation (Snowdon & Hausberger, 1997). Gros-Louis, West, Goldstein, and King (2006) thus argued that vocal development in human infants is shaped by social interactions, while acknowledging that the specific links between social context and prelinguistic vocal development are understudied (Vihman, 1996). Hence, immature individuals might obtain competitive advantages if they interact more frequently with conspecifics, which will also enhance their communicative development. Chimpanzee infants of highly social mothers thus get a head start in life.

Interactional Experience with Mothers

Interestingly, gestural signalling was not associated with previously experienced interactions with mothers. However, this result does not necessarily contradict the assumption that mothers positively influence their infants' communicative development (Bard, 1992; Luef & Liebal, 2012; Maestripieri & Call, 1996). Owing to the high familiarity and the predictable outcomes within the mother–infant dyad, it seems plausible that relatively few signals are needed to enable mutual understanding. In interactions with the mother, an infant learns in a safe, cooperative environment that certain behaviours can act as signals and has the opportunity to test and experience them. During interactions with nonmaternal conspecifics, gestures are likely to be more frequent since the environment of mutual understanding, which have so far only been established between mothers and their infants, still needs to be created and shaped. Importantly, infants of social mothers can accumulate much more experience with conspecifics, exercise and test signals, and might thus have a head start in the complex social world of chimpanzees. To investigate the issue of 'mutual understanding', one needs to specifically measure communicative success in gestural interactions, which would be an important avenue of research.

Moreover, our findings corroborate in many ways the empirical framework for gestural development obtained thus far. First, Fröhlich et al. (2016a) recently demonstrated that both visual and audible gesturing for play solicitation, a major communicative context in infants, directed at mothers was relatively rare, while tactile means were employed more frequently. Given the mother–infant attachment and the stable association of this unit, we argued that physical actions and tactile gestures that involve

body contact and are of relatively high risk might be reserved for secure and familiar interactions, i.e. those with mothers.

Second, very little work has addressed the mechanisms through which mothers could play a role in the development of their offspring's communicative development. Schneider, Call, and Liebal (2012b) argued that imitation of mothers is a very unlikely learning mechanism underlying gesture acquisition, since infants share a considerably larger portion of their gestural repertoire with individuals of their age group than with mothers. Thus, the mother does not act as a model for gestural production and usage; rather, peers of the same group do (Schneider et al., 2012b). Moreover, a substantial portion of gesture types exchanged within the mother–infant dyad is produced 'one-way', that is only by one dyad member (Fröhlich, Wittig, et al., 2016b; Halina et al., 2013). In line with these results, Hobaiter and Byrne (2011a) found no evidence for 'matrisyncratic' gestures, that is gestures only observed in individuals of a single maternal family line, in the repertoires of wild chimpanzees.

Furthermore, our findings support results from a recent study on mother–infant joint travel in wild chimpanzees (Fröhlich, Wittig, et al., 2016b), where we proposed that gestures are acquired via 'social negotiation' (sensu Plooi, 1978; Wittgenstein, 1953). According to this theory, gestures are created in social interactions resulting in a shared understanding that specific behaviours can be used to achieve communicative goals and carry distinct meanings linked to particular social contexts (Fröhlich, Wittig, et al., 2016b). In addition, we (Fröhlich, Wittig, et al., 2016a) recently examined the impact of demographic factors and relationships on play-soliciting signals in individuals of the same communities with results also strongly supporting the important role of nonmaternal conspecifics for shaping gestural production and use. Social experience with conspecifics is crucial for creating the communicative tool kit of an individual, and this reliance on a developmental period implies that learning plays a major role in the acquisition of meaningful signalling. Gestural ontogeny in great apes might thus resemble an ancient 'layer' of language (Levinson & Holler, 2014) still present in the speech and gesture of modern humans (Plooi, 1978), possibly constituting an example of ontogeny recapitulating phylogeny. It also demonstrates that the developmental approach is a critical tool for revealing cognitive prerequisites underlying both human and ape communication systems.

Maternal Proximity and Gestural Development

Concerning the influence of mothers' proximity on gestural development, we found no effect on the gestural parameters analysed. These results do not support our first prediction, suggesting that gestural signalling should increase with lower maternal proximity, owing to the gain in spatial independence on behalf of the infants. We also found no support for the second prediction, namely that gestural development in chimpanzees is highly dependent on the proximity (the 'security range') to their respective mothers. In the early stage of development, when infants permanently cling to their mother's body, there is little need for gestural signalling. However, the mother may provide an environment in which the infant is confident to exercise gestural signals with conspecifics. Our results showed that the need for communication via visual and audible gestures arises only later in life, that is at the age of 1–2 years when the infant begins to frequently move independently and interact with various social partners (see also van Lawick-Goodall, 1967). Previous studies suggested that the referential triangle, incorporating distant objects into the relationship between a signaller and the recipient of the gesture (e.g. Butterworth, 2003), only opens up when infants become more

spatially independent and leave their mother's immediate vicinity (Bard et al., 2005; van Lawick-Goodall, 1967). Leavens, Hopkins, and Bard (2008) proposed that the reported differences between chimpanzees and human infants concerning distinct gestures such as pointing and explicit reference arise from the fact that chimpanzees, in contrast to humans, develop independent locomotor competence long before the onset of means-ends reasoning (i.e. knowledge of causal connections between courses of actions and their results). This is remarkably different from infant raising in so-called human WEIRD societies (Western, Educated, Industrialized, Rich and Democratic; Henrich, Heine, & Norenzayan, 2010), where caretakers expose their children to distance between them from a young age. It has been argued that cross-cultural differences in early exposure to referential space resulted in temporal shifts in the ontogeny of explicit reference (Leavens et al., 2008). Moreover, cross-cultural research has demonstrated that this distal parenting style nurtures mutual gaze and object stimulation, and has substantial consequences for the development of self-regulation and self-recognition (Keller et al., 2004). The present study may thus stimulate further cross-species comparisons by using within- and between-subject designs to better understand which factors drive the development of communicative complexity. Such an approach might also help to shed light on differences and similarities in cognitive abilities underlying communicative skills.

Sex Differences in Gesture Use

Concerning sex effects on gestural production, we found a marked sex difference for gesture frequency and repertoire sizes of infants. While, to our knowledge, there is no explicit evidence that gestural repertoire sizes in humans or great apes differ between males and females (however, see Nicoladis, Pika, Yin, & Marentette, 2007 for human sex differences regarding gestural frequencies), sex differences in chimpanzees have been found at the Gombe community, Tanzania for the domains of sociability (Lonsdorf, Anderson, et al., 2014) and social learning abilities (Lonsdorf, 2005; Lonsdorf, Eberly, & Pusey, 2004). In addition, investigations of sex differences concerning handedness during gesturing have provided mixed results (Hopkins & Leavens, 1998; Hopkins et al., 2005, 2012; Hopkins & de Waal, 1995). With regard to play interactions and sociability, our study corroborates findings of Lonsdorf, Andersson et al. (2014), Lonsdorf, Markham et al. (2014) at Gombe who reported sex differences in social, but not solitary play, with males dedicating more time at earlier ages to social play than females. In addition, Lonsdorf, Andersson et al. (2014), Lonsdorf, Markham et al. (2014) documented sex differences in sociability, showing that male infants interacted with significantly more individuals than female infants did, with a particular bias towards adult males. This has been discussed with regard to the crucial role of socialization in young chimpanzee males given the importance of social dominance in adulthood and reflecting the adult reproductive strategies (Muller & Mitani, 2005). Studies from other field sites are needed to verify whether an early sex difference in sociability is a universal species characteristic or whether it is, like some other behavioural patterns such as weak social bonds among females, intergroup killing and infanticide (Gruber & Clay, 2016), more pronounced in the eastern subspecies.

In sum, our results provide the first evidence that the documented early sex difference in sociability is also apparent in the development of gestural communication, with differences in gestural behaviour between males and females possibly reflecting differential importance of early socialization (Murray et al., 2014). These findings further corroborate the crucial role of interactional experience with different social partners for communicative development.

Conclusion

The present study examined gestural development and its relationship to sociocomotor development in chimpanzee infants using a novel combination of behavioural and scan sampling, thereby allowing for within-/between-subject and -site comparisons. Overall, our study demonstrated that social interactions experienced by chimpanzee infants play vital roles for their communicative development. Mastering flexible, intentional and 'meaningful' gestural communication is preceded by a developmental trajectory within which infants receive crucial input from social stimuli. Thus, learning experiences throughout ontogeny might crucially drive the appropriate usage in social contexts. Moreover, we have provided hitherto undocumented evidence that different roles of early socialization for chimpanzee males and females might be reflected in the development of gestural communication. Our study thus demonstrates the benefit of using a comparative, developmental approach to gain insight into the complexity inherent to specific communication systems. We hope to have stimulated research into the socioenvironmental constraints great apes are exposed to throughout their communicative development. In turn, this will hopefully shed light on how human language was preceded by, or coevolved with, the flexibility and goal-directed use of gestures (Levinson & Holler, 2014; Smit, 2014).

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Appendix

Table A1
 Gesture types produced in chimpanzees to solicit food sharing identified in this and other wild communities: Sonso (Hobaiter & Byrne, 2011a), Gombe (Goodall, 1986) and Mahale (Nishida, Zamma, Matsusaka, Inaba, & McGrew, 2010)

Gesture type	Definition (this study)	Sonso	Gombe	Mahale
Tactile				
Bite ^a	Signaller holds parts of recipient's body between the teeth	Bite	Mouthing	Mouth
Finger in mouth ^a	Signaller inserts one or more fingers into mouth of recipient	–	Push finger into mouth	Push finger into mouth
Grab ^a	Signaller closes fingers firmly around a body part of recipient	Grab	Grab	Grab
Hold onto ^{a,b}	Signaller grasps and maintains physical contact with recipient, without pulling or pushing involved	Grab and hold	–	Grasp hand
Mouth beg	Signaller puts lips to lips or hand of feeding recipient	–	Beg mouth-to-mouth	Mouth for begging
Mouth stroke	Signaller puts fingers repeatedly over the mouth region of recipient	Mouth stroke	–	–
Touch, long ^a	Signaller makes long (>2 s) contact with recipient using palm and/or fingers	Hand on	Touch	Touch
Touch, short ^{a,b}	Signaller makes short (<2 s) contact with recipient using palm and/or fingers	Touch other	Touch	Touch
Pull ^a	Signaller moves recipient's body part towards himself	Pull	Pull	Pull
Visual				
Grab pretend	Signaller makes grabbing movement towards food/recipient without touching	–	–	–
Hand bent ^b	Signaller holds hand and arm in a vertical plane, with bent wrist, back of the hand directed to food	–	–	Extend hand to beg
Hover ^b	Signaller's hand is circling or held close (<15 cm) to food, palm directed towards it	–	–	–
Look ^a	Signaller gazes at recipient (>2 s)	Look	Wait	Beg
Palm-up ^b	Signaller stretches out hand palm upwards towards food/mouth of recipient	–	–	–
Peer	Signaller stares intently at recipient, moving head close (<15 cm).	Look	Putting face close	Peer
Reach ^{a,b}	Signaller extends arm towards recipient/food	Reach	Extend hand	Extend hand

^a Gesture types reported in Fröhlich, Wittig, et al. (2016b) for joint travel and/or Fröhlich, Wittig, et al. (2016a) for play contexts in chimpanzees.

^b Gesture types reported in Wilkinson et al. (2012) for meat-sharing episodes in chimpanzees.