



What Role Do Mothers Play in the Gestural Acquisition of Bonobos (*Pan paniscus*) and Chimpanzees (*Pan troglodytes*)?

Christel Schneider · Josep Call · Katja Liebal

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Abstract Contemporary research hypothesizes that biological inheritance and ontogenetic factors shape the development of gestural communication in nonhuman great apes. However, little is known about the specific role that mothers play in the acquisition of their infants' gestures. We observed 6 bonobo (*Pan paniscus*) and 4 chimpanzee (*Pan troglodytes*) mother–infant dyads and recorded their gesture types and frequency. We analyzed all behavioral contexts in which gestures occurred as well as the play context alone. Infants of both species were unlikely to share gestures with their mother or unrelated adult females. However, gestural sharing was prevalent within age groups. Within and across species, infant–infant and mother–mother groups were homogeneous regarding the types of gestures they shared, although there was individual variation in the frequency of gesture use. Our findings provide limited evidence that infants learned their gestures by imitating their mothers. Phylogenetic influences seem to be vital in gestural acquisition but, we suggest, repertoire development cannot be disentangled from individual social encounters during life.

Keywords Bonobo · Chimpanzee · Communication · Gesture acquisition · Mother–infant dyad

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C. Schneider · K. Liebal
Department of Evolutionary Psychology, Freie Universität Berlin, 14195 Berlin, Germany

C. Schneider · K. Liebal
Department of Developmental and Comparative Psychology,
Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

C. Schneider (✉) · K. Liebal
Department of Psychology, University of Portsmouth, Portsmouth PO1 2DY, UK
e-mail: schneide@eva.mpg.de

J. Call
Department of Developmental and Comparative Psychology,
Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

Introduction

Currently, there is a lively debate about the relative importance of biological inheritance and ontogenetic factors in the acquisition of gestural communication in nonhuman great apes (Hobaiter and Byrne 2011; Liebal and Call 2011). One source of evidence supporting the biological inheritance of gestures comes through observing young apes that developed species-typical gestures in the absence of role models, i.e., they were unable to observe older conspecifics. Signals in these deprived contexts, such as *chest beat* in gorillas (*Gorilla gorilla*), strongly resemble those performed by conspecifics living in natural group compositions (Redshaw and Locke 1976). An alternative approach is to study more typically developing species groups. For example, an analysis of captive and wild gorillas suggests that most of their gestures belong to a universal species-typical pool and that apparent repertoire differences between individuals and groups can be explained by varying ecological conditions (Genty *et al.* 2009). Genetically channeled gestural overlap has also been reported across species. A recent study of wild chimpanzees (*Pan troglodytes*) found that gestures were not only shared within community members, but they were also comparable with many gestures previously recognized across the 3 genera chimpanzees, gorillas, and orangutans (Hobaiter and Byrne 2011).

Evidence for the importance of ontogenetic influences in the gestural acquisition process comes in the form of individual learning captured in a series of studies on captive chimpanzee youngsters over a 12-yr period (Tomasello *et al.* 1985, 1989, 1994, 1997). Through a process of ontogenetic ritualization (described as conventionalization by Smith 1977) a signal develops as 2 individuals shape each other's behavior in repeated interactions (Tomasello and Call 1997). A noncommunicative behavior gains a communicative function through anticipation of the socially interacting individuals over time. For example, a chimpanzee youngster slaps her partner while playing. After several repetitions of this behavior the conspecific recognizes the signal and anticipates the play behavior. The ritualization is complete when the youngster raises its arm, not to perform the physical act of slapping but to demonstrate an abbreviated *arm raise* gesture to invite play (Tomasello and Call 1997). Support for this process underpinning gestural acquisition comes from studies that have witnessed the invention of new signals through social interactions and the highly variable repertoires observed among individuals in species groups (Call and Tomasello 2007b). Captive bonobos (*Pan paniscus*: Pika *et al.* 2005b), chimpanzees (Tomasello *et al.* 1985), gorillas (Pika *et al.* 2003); and orangutans (*Pongo pygmaeus*: Liebal *et al.* 2006) all show idiosyncratic gestures, i.e., signals that are performed by only 1 subject.

Gestures can also be acquired through imitative learning (Zentall 2006). Here individuals learn gestures by observing and subsequently replicating behaviors from parents (vertical transmission), peers (horizontal transmission), or unrelated older group members (oblique transmission; Cavalli-Sforza and Feldman 1981). Supporting evidence is provided by group-specific gestures, i.e., gestures that are used by members in one group but not in other groups. For example, Liebal *et al.* (2006) observed the signal *offer arm with food pieces* in a single group of captive orangutans (for similar observations in captive gorillas and bonobos, see Pika *et al.* 2003, 2005b).

Study of the mother–infant relationship is likely to elucidate important information about the origin of gestures. All great apes have extended periods of immaturity (Pereira and Fairbanks 2002), and hence the mother–infant dyad is characterized by a long-lasting and intense relationship (Hoff *et al.* 1981; Plooij 1978, 1984; van Lawick-Goodall 1967). For example, in orangutans and chimpanzees, the mother plays an important role in the development and facilitation of foraging skills (Bard 1992; Hirata and Celli 2003; Jaeggi *et al.* 2010; Lonsdorf 2006; van Schaik 2004). Mothers are also the most important social partner when infants begin to gesture (which is, broadly speaking, between 1 and 1.5 yr of life in nonhuman great apes; Plooij 1978; Schneider *et al.* 2011) and are essential during an infant’s socialization process (King 2004; Maestripieri and Call 1996).

However, gestural research has neglected the mother–infant dyad context. In the only systematic investigation of the mechanisms underlying gestural acquisition, Cartmill (2008) compared repertoire overlaps among 8 orangutan youngsters (7 aged 10–25 mo, and 1 aged 30–48 mo) and their mothers (including 2 foster, i.e., nonbiological, mothers). The association between infant and caregiver was important to the imitative learning of gestures. Infants shared more gestures with their mother or adoptive mother than they did with other adult female group members. This is in contrast to chimpanzees, for which peers seemed to be more important than the mother in gestural development (Tomasello *et al.* 1989, 1994).

Our objective in the present study was to investigate more directly the role played by bonobo and chimpanzee mothers in the gestural development of their infants. We used an observational method to contrast, within and between *Pan* spp., the following dyads: infant–(biological) mother, infant–unrelated adult female, infant–infant, and mother–mother. For each dyad observed, we recorded and compared the types of gestures exhibited and their frequency. This allowed us to address the following 3 issues: 1) We explored the role that bonobo and chimpanzee mothers played in their infants’ gestural acquisition by examining the extent to which gestures were shared. A significant overlap within this dyad would emphasize the importance of imitative learning in gestural acquisition. 2) We investigated the extent that peers (infant and mother age group) shared gestures within and across the 2 *Pan* spp. Age group overlap across species would signify the importance of phylogenetic influences in the gestural acquisition process. 3) We examined the gesture frequency for all dyads observed to capture individual variability and the importance of social encounters in early life.

Methods

Subjects

We observed 6 bonobo (*Pan paniscus*) and 4 chimpanzee (*Pan troglodytes*) infants in their first 20 mo of life (Table I). All infants were born in captivity, lived in socially housed groups in 6 European zoos, and were raised by their biological mothers. The group sizes ranged between 5 and 8 individuals in bonobos and between 11 and 20 individuals in chimpanzees (for details of the age composition of each group see Table I).

Table 1 Details of the focal subjects

Species	Infant	Sex	Date of birth	Size and age distribution of group (at infant's birth)	Observation regularity	Observation period (age in mo)	Total observation time (h)	Location
Bonobo	Habari	Male	29/01/06	8 (5A, 1S, 2 ^b)	Biweekly	13–20	8	Mechelen
	Hongo	Male	25/02/06	8 (5A, 1S, 1I+1 ^b)	Biweekly	12–20	9	Mechelen
	Huenda	Female	06/07/06	8 (5A, 1S, 2I)	Biweekly	7–16	10	Mechelen
	Kivu	Male	24/02/07	5 (4A, 1S)	Biweekly	2–20	19	Berlin
	Luiza	Female	27/01/05	5 (2A, 3S)	Weekly	8–20	13	Leipzig
Chimpanzee	Nayembi	Female	26/04/06	8 (4A, 2S, 2 J)	Biweekly	12–19	8	Apeldoorn
	Gihneau	Male	29/12/05	20 (16A, 3S, 1I)	Biweekly	14–19	6	Arnhem
	Kara	Female	23/06/05	17 (9A, 2S, 3 J+1J ^a , 1I+1I ^b)	Weekly	2–20	19	Leipzig
	Kofi	Male	07/07/05	17 (9A, 2S, 3 J+1J ^a , 2I)	Weekly	2–20	19	Leipzig
	Nafia	Female	10/06/06	11 (6A, 3S, 2I)	Weekly	10–20	11	Münster

A = adult (≥ 10 yr); S subadult (6–9 yr); J juvenile (2.6–5 yr); J infant (0–2.5 yr)

^a Left the group during the study

^b Born during the study

Observational and Coding Procedure

C. Schneider and research assistants videotaped the observations between July 2005 and August 2008. We used focal animal sampling to record the infants' social interactions (Altmann 1974). We observed each infant either once every week or twice every second week, which resulted in 4 sessions (each lasting 15 min) and 1 h of video footage per subject per month. The time of the observations varied between 08:30 h and 19:00 h, with sessions for every subject distributed across the apes' diurnal activity. We observed each infant for a period of between 6 and 19 mo during its first 20 mo of life (Table 1). Overall, we recorded bonobos for 67 h and chimpanzees for 55 h. We incorporated a subset of coded data (which accounted for one third of the whole data set) from a research project investigating gestural onset and early use in nonhuman great apes (Schneider *et al.* 2011).

We defined a gesture as a motoric action (performed by head, limbs, or whole body) that fulfilled the following criteria: 1) it was directed to a particular recipient, accompanied by orienting body toward recipient and gazing at it; adopted from Call and Tomasello (2007b) and Wetherby *et al.* (1988); 2) it served a functional purpose (Call and Tomasello 2007b); and 3) the sender needed to show anticipation of the recipient's reaction accompanied by gazing (Bates *et al.* 1975; Bruner 1981; Tomasello *et al.* 1994). This definition excludes simple mechanical actions produced to achieve a desired outcome without leaving the recipient the choice of action, e.g., to relocate another individual by applying physical force (Call and Tomasello 2007b). Gestures could be tactile, visual, or auditory.

We recorded all gestures produced by the focal individuals (directed to mother or other group members) and their mothers (directed to the infant or other group members). We noted mothers' gestures whenever they were near the infant and therefore in view of the camera. To ensure that comprehensive repertoires were captured for the mothers (which were not focal individuals), we analyzed, where available, additional video footage of their gestural behavior before the infants' first gestures (on average infants in the current sample started gesturing at 11 mo). For each gesture we coded the following variables: sender and recipient, sex and age group (infant: 0–2.5 yr; juvenile: 2.6–5 yr; subadult: 6–9 yr; adult: ≥ 10 yr), gesture modality (tactile: signal was transferred by initiating body contact with recipient; visual: signal was transferred over a distance via particular body movements or postures; auditory: signal was transferred via the acoustic channel but was nonvocal), gesture type, and behavioral context as judged by the available pre- and postinformation that accompanied the sender's signal (see electronic supplementary material [ESM] Table SI for behavioral descriptions of gesture types and contexts).

Interobserver Reliability

C. Schneider coded all video footage. To determine reliability, a naïve second person coded 20% of randomly chosen infant and mother gestures. We used Cohen's κ to measure the degree of concordance between raters for gesture type and behavioral context (Altman 1991). However, κ could not be computed when we identified unbalanced coding between raters, resulting in asymmetry in the table, e.g., one rater used codes 1–3, whereas the other rater never used code 1 at all. Here, we used a

permutation procedure to determine the coefficient (Manly 1997; software written by R. Mundry). First, the original agreement between the 2 observers was established. The codes of one observer were then randomized and the agreement was measured again. In total we conducted 1000 randomizations (with the original data included as 1 permutation). Afterwards we compared the original agreement with the distribution of agreements derived from the permutations. We determined the p -value by the proportion of permutations that showed agreement at least as large as the original data. We determined the κ coefficient as usual [$\kappa = (\text{observed agreement} - \text{expected agreement}) / (1 - \text{expected agreement})$], whereby the expected agreement was the average agreement revealed from truly permuted data. By applying this procedure, we retained the information from every observation and ensured that κ was an appropriate measure of the reliability of the original codes. For the gesture types, the κ values ranged between 0.76 (mother) and 0.82 (infant), and 0.73 (mother) and 0.73 (infant) for the behavioral contexts. All κ values were highly significant ($p < 0.002$), and according to Altman (1991) equated to a good or very good level of agreement.

Data Analyses and Statistics

We applied the Kendall rank correlation coefficient tau (τ) to correlate the frequencies with which distinct gestures occurred in 2 individuals of a given dyad. We determined the correlation twice per dyad: once based on only the gestures shown by both individuals (*only both* data set) and once including each gesture shown by at least one of the 2 individuals, i.e., their entire repertoires (*at least once* data set). A T of -1 indicates that gestures frequently performed by one individual were never shown by the other individual, whereas a T of $+1$ indicates that relative frequencies by which the 2 individuals exhibited the gestures were in perfect agreement. We calculated the DICE-coefficient C_D (Dice 1945) to obtain a measure of how similar the repertoires of 2 individuals were [with $C_D = 2 \times \text{number of gestures common for subject A and B} / (\text{total number of gestures shown by subject A} + \text{total number of gestures shown by subject B})$]. This coefficient indicates the proportion of shared gestures used in a dyad and ranges between 0 and 1; 0 indicates that two individuals did not share any gesture and 1 indicates a perfect match of gesture repertoires in a dyad.

In the case of the correlation data sets (*only both* and *at least once*), we applied Fisher's omnibus tests (Haccou and Meelis 1994) to ascertain whether single significant p -values were spurious. Here the p -values of the correlation coefficients were integrated into a single χ^2 -distribution, where the degrees of freedom were twice the number of p -values incorporated. We then tested whether correlations between frequencies of gestures differed among dyad-types (infant–own mother *or* infant–other mothers) as well as among species. To do so, we undertook a repeated-measures ANOVA for the proportions of shared gestures (DICE) and for each correlation data set (*only both* and *at least once*), into which we included species as a between-subjects factor and dyad-type as a within-subjects factor.

Next, we compared the similarities between repertoires among different groups of dyads (DICE coefficients of shared gestures and correlations between gesture frequencies). First, we conducted comparisons between infant–infant, mother–mother, and infant–mother (own and other) dyads. We considered only bonobos for this analysis because they were

the only species with a large enough sample size. If such a test is significant it could, for instance, indicate that repertoires of infants are particularly homogeneous, i.e., show larger similarity with one another rather than with mothers, or mothers with one another. Second, we compared bonobo–bonobo, chimpanzee–chimpanzee, and bonobo–chimpanzee infant dyad groups. Last, we repeated this comparison for mothers (bonobo–bonobo, chimpanzee–chimpanzee, and bonobo–chimpanzee). These 3 analyses could not be conducted using standard tests because the data were not independent, i.e., each individual was involved in several dyadic measures of similarity. Hence, we used a permutation test (Adams and Anthony 1996; Manly 1997), similar to a Mantel test for matrix correlation (Sokal and Rohlf 1995). In the present analysis, one matrix denoted the dyadic similarity, e.g., the correlation between frequencies by which gestures occurred in the 2 subjects of a dyad; the other matrix represented the dyad type, e.g., infant–mother, mother–mother, etc. The test statistic consisted of the sum of the squared differences between mean similarity measures per dyad-type and the mean similarity measures of all dyads. We achieved permutations by simultaneously randomizing rows and columns of 1 of the 2 matrices. By conducting 1000 permutations (into which the original data were included as 1 permutation), we obtained the sampling distribution of the test statistic under the assumption of a true null hypothesis. Finally, we estimated the p -value as the proportion of test statistics in the sampling distribution being at least as large as that of the original data.

We calculated the repeated-measures ANOVAs using SPSS 15.0. We computed the Fisher's omnibus test by hand, and for the matrix permutation test, we used a script (written by R. Mundry) for R 2.9.1 (R Development Core Team 2009).

Results

Description of Mother–Infant Gestural Repertoires

We analyzed a total of 1269 gestures (comprising 39 distinct gesture types). The 6 bonobo infants produced 247 gestures (consisting of 21 types) and their mothers 561 gestures (26 types). The 4 chimpanzee infants employed 184 gestures (25 types) and their mothers 277 gestures (22 types; see ESM Table SI for signal types observed and corresponding sensory domain in infants and mothers of each species).

Infant repertoires ranged from 5 to 17 gesture types in bonobos and from 10 to 17 gesture types in chimpanzees. Mother repertoires consisted of 11 to 18 gesture types in bonobos and 9 to 14 in chimpanzees (Table II).

Similarity of Repertoires Within Mother–Infant Dyads

Overall, p -values derived from the Kendall correlation coefficients (Table III) were significant in all infant–own mother and infant–other mothers dyad types (Fisher's omnibus test: $\chi^2=108.79$, $df=78$, $p=0.012$). Infants were dissimilar from their own mothers and other mothers concerning the frequency of gestures that were employed by ≥ 1 dyad member (*at least once* data set). The coefficients ranged from 0.01 to -0.58 (infant–own mother) and -0.14 to -0.54 (infant–other mothers); the

Table II Repertoire sizes of infants and mothers in bonobos ($N=6$) and chimpanzees ($N=4$) and the number of gesture types shown by each individual alone, and common to both

Species	Mother–infant dyad	Repertoire size		Infant only	Mother only	Both
		Infant	Mother			
Bonobo	Djanao–Habari	17	14	8	5	9
	Hermien–Huenda	5	13	2	10	3
	Hortense–Hongo	10	13	8	11	2
	Liboso–Nayembi	10	12	6	8	4
	Ulindi–Luiza	12	18	5	11	7
	Yala–Kivu	8	11	7	10	1
Chimpanzee	Fraukje–Kara	11	14	5	8	6
	Gaby–Gihneau	14	9	10	5	4
	Ulla–Kofi	17	12	11	6	6
	Yola–Nafia	10	10	5	5	5

corresponding p -values were significant when we compared infants with their own mothers (Fisher's omnibus test: $\chi^2=43.07$, $df=20$, $p=0.002$) and other mothers ($\chi^2=41.61$, $df=20$, $p=0.003$; Table III). The correlations for gestures that were employed by both members of a dyad (*only both* data set), however, were nonsignificant in

Table III Kendall rank correlation coefficients (T) and corresponding p -values between infant–own mother and infant–other mothers

Species	Infant	<i>At least once</i> data set				<i>Only both</i> data set			
		Own mother		Other mothers ^a		Own mother		Other mothers ^a	
		T	p	T	p	T	p	T	p
Bonobo	Habari	0.01	0.976	−0.41	0.034	−0.10	0.741	−0.24	0.549
	Hongo	−0.53	0.003	−0.38	0.182	−1.00	1.000	−0.21	0.269
	Huenda	−0.10	0.664	−0.14	0.288	0.33	1.000	0.38	0.806
	Kivu ^b	−0.58	0.003	−0.47	0.101	—	—	−0.33	1.000
	Luiza	−0.19	0.272	−0.30	0.226	−0.16	0.634	−0.10	0.583
	Nayembi	−0.30	0.124	−0.23	0.261	−0.91	0.071	−0.23	0.837
Chimpanzee	Gihneau	−0.35	0.068	−0.38	0.073	0.24	0.655	−0.16	0.535
	Kara	−0.21	0.259	−0.54	0.007	−0.39	0.304	−0.61	0.740
	Kofi	−0.21	0.226	−0.14	0.463	0.21	0.559	0.00	0.671
	Nafia	−0.16	0.460	−0.25	0.345	−0.60	0.166	−0.22	0.613

^a The reported significance levels are based on the mean values for all possible infant–other mothers dyads (bonobos: $N=5$, chimpanzees: $N=3$)

^b The bonobo infant Kivu shared only 1 gesture with his mother. He was therefore excluded from all *only both* analyses because a coefficient could not be calculated

infant–own mother dyads (Fisher’s omnibus test: $\chi^2=14.79$, $df=18$, $p=0.676$) and infant–other mothers dyads ($\chi^2=9.32$, $df=20$, $p=0.979$; Table III). Here, the corresponding coefficients ranged from 0.33 to -1.00 (infant–own mother) and 0.38 to -0.61 (infant–other mothers).

A repeated-measures ANOVA on each correlation data set (*only both* and *at least once*) with the factors species (bonobo vs. chimpanzee) and type of dyad (infant–own mother vs. infant–other mothers) indicated no differences between bonobo and chimpanzees (*only both*: $F(1,7)=.022$, $p=0.887$; *at least once*: $F(1,8)=.069$, $p=0.800$), or dyad-type (*only both*: $F(1,7)=.459$, $p=0.520$; *at least once*: $F(1,8)=1.137$, $p=0.317$). We found no significant interaction between these factors (*only both*: $F(1,7)=2.29$, $p=0.174$; *at least once*: $F(1,8)=.202$, $p=0.665$). Infants of both species showed a similar frequency of gesture occurrences (concerning gestures that occurred in both individuals or in ≥ 1 dyad member) with unrelated adult females as they did with their own mothers (Table III). A further repeated-measures ANOVA on the proportions of shared gestures, with the factors species (bonobo vs. chimpanzee) and type of dyad (infant–own mother vs. infant–other mothers), also indicated no difference between bonobos and chimpanzees ($F(1,8)=1.009$, $p=0.345$) or dyad types ($F(1,8)=.430$, $p=0.530$). Again, we found no significant interaction between these factors ($F(1,8)=0.493$, $p=0.503$).

Further Comparison of Dyad Groups

Permutation analysis revealed no significant differences in frequency of occurrence of gestures for both individuals of a dyad in bonobos ($p=0.221$; correlations based on *only both* data). However, the comparison of repertoires yielded a significant overall effect when analyzing proportions of shared gestures in a dyad ($p=0.001$; Fig. 1a), as well as the correlations between frequencies of gestures that were shown by ≥ 1 of 2 dyad members ($p=0.004$; Fig. 1b). *Post hoc* tests revealed that the homogeneity in terms of shared gestures and gesture frequency in the infant–infant group differed significantly from that in the infant–mother group (DICE: $p=0.001$; *at least once*: $p=0.003$). Likewise, the mother–mother group differed in their homogeneity from that of the infant–mother group for each data set (DICE: $p=0.001$; *at least once*: $p=0.008$). The infant–infant and mother–mother groups, however, did not differ significantly from each other (DICE: $p=0.649$; *at least once*: $p=0.171$). For both data sets therefore, infant–infant and mother–mother dyads showed more homogeneity than mother–infant dyads. We observed a similar pattern in chimpanzees (Fig. 2) but because of the small sample size, a test of significance was not possible.

Comparisons of the bonobo–bonobo, chimpanzee–chimpanzee, and bonobo–chimpanzee infant dyad groups indicated no significant differences for any of the 3 data sets (*only both*: $p=0.256$; *at least once*: $p=0.194$; DICE: $p=0.189$; Table IV). The shared types and frequencies of gestures for bonobo and chimpanzee infants did not differ significantly among the 3 groups, i.e., neither of the 2 species was more homogeneous than the other or the interspecies dyads. We found no indication of a significant effect when performing the same analyses for mothers (*only both*: $p=0.416$; *at least once*: $p=0.956$; DICE: $p=0.911$; Table IV).

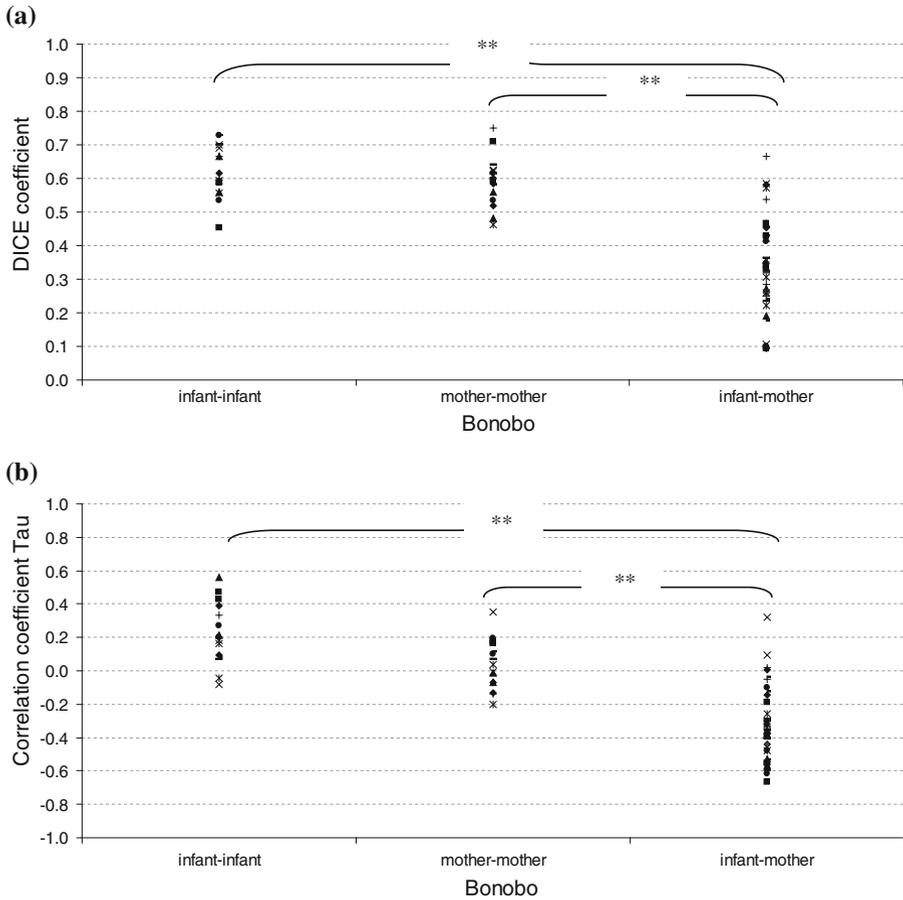


Fig. 1 Repertoire similarities for bonobos in the 3 dyad groups infant–infant ($N=15$), mother–mother ($N=15$), and infant–mother ($N=36$). (a) DICE coefficients. (b) coefficients of *at least once* data set.

Focusing on Play-Related Gestures

To ascertain whether the observed gestural similarities and dissimilarities depended on behavioral context, we analyzed gesture use by context, e.g., play, ingestion (ESM Table SI). However, in doing so, the numbers of gestures available for analysis decreased considerably and play was the only context in which there was a sufficient amount across species and age groups to allow meaningful analysis. We restricted the analyses to the proportions of shared gestures (DICE) for the same reason and no longer conducted frequency analyses. After the calculations of the DICE coefficients we conducted a repeated-measures ANOVA and permutation tests in the same way as we did with the overall data set.

Overall, we observed 498 play-related gestures (comprising 30 gesture types). The 10 infants produced 246 play gestures (24 types) and their mothers 252 (17 types; see ESM Table SI for number of gestures observed in play in infants and mothers of each species). Bonobo infants used 4–13 gesture types, and chimpanzee infants 6–11

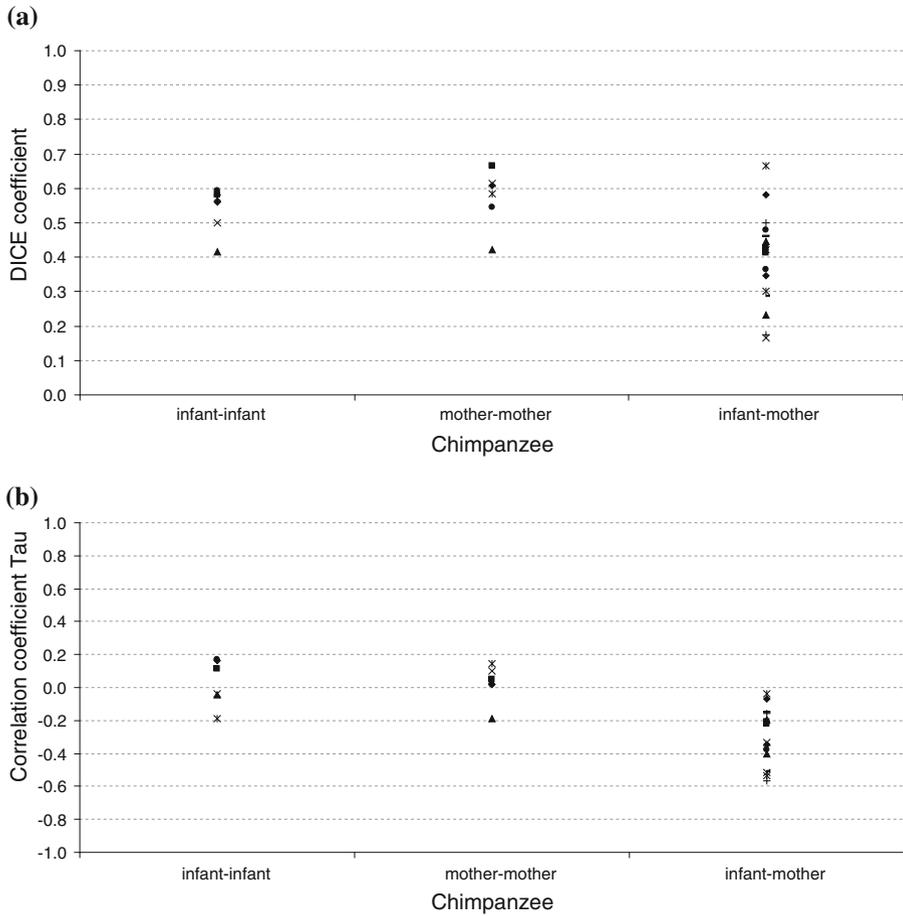


Fig. 2 Repertoire similarities for chimpanzees among infant–infant ($N=6$), mother–mother ($N=6$), and infant–mother dyads ($N=16$). **(a)** DICE coefficients. **(b)** coefficients of *at least once* data set.

types. Bonobo mothers showed 4–10 gesture types, while chimpanzee mothers used 1–8. Of the 4 chimpanzee mother–infant dyads, only a single dyad shared any

Table IV Mean coefficient values for *only both* and *at least once* correlations and DICE data set

Data set		Species comparison		
		Bonobo– bonobo	Chimpanzee– chimpanzee	Bonobo– chimpanzee
Infants	Only both (T)	0.09	0.38	0.09
	At least once (T)	0.22	0.03	0.14
	DICE C_D	0.62	0.54	0.58
Mothers	Only both (T)	0.20	0.05	0.28
	At least once (T)	0.04	0.02	0.05
	DICE C_D	0.59	0.57	0.59

gestures (2 types) with each other. In bonobos, 4 of 6 mother–infant dyads shared gestures (1–5 types per dyad).

A repeated-measures ANOVA with the factors *species* and *dyad-type* (infant–own mother vs. infant–other mothers) showed no difference between species ($F(1,8)=2.226, p=0.174$) or dyad types ($F(1,8)=0.207, p=0.661$), and no significant interaction between factors ($F(1,8)=0.719, p=0.421$). Infants of both species shared a similarly low number of gestures with unrelated adult females (mean DICE coefficients; bonobo=0.21, $N=6$; chimpanzee=0.14, $N=4$) as they did with their own mothers (bonobo=0.23, chimpanzee=0.07).

When comparing shared play-related gestures exhibited in dyad groups (infant–infant, mother–mother, and infant–mother), we found a significant overall effect for bonobos ($p=0.001$; Fig. 3a). *Post hoc* permutation tests revealed that the homogeneity in terms of shared play gestures in the infant–infant group differed significantly from that in the infant–mother group ($p=0.001$). Likewise, the mother–mother group differed in its homogeneity from that of the infant–mother group ($p=0.001$). The

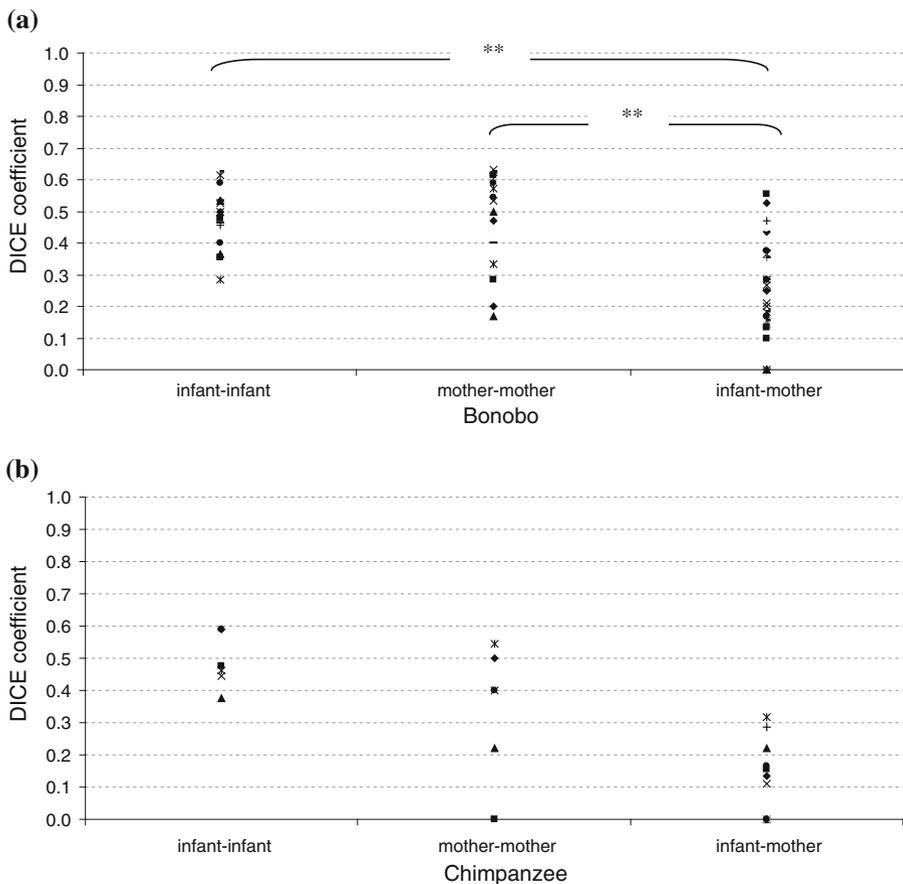


Fig. 3 Similarities of play gestures (DICE coefficients) for (a) bonobos in the 3 dyad groups infant–infant ($N=15$), mother–mother ($N=15$), and infant–mother ($N=36$). Also presented are similarities of play gestures for (b) chimpanzees among infant–infant ($N=6$), mother–mother ($N=6$), and infant–mother dyads ($N=16$).

infant–infant and mother–mother groups, however, did not differ significantly from each other ($p=0.917$). Conclusively, infant–infant and mother–mother dyads showed more homogeneity than mother–infant dyads (see Fig. 3b for chimpanzees).

Comparisons of bonobo–bonobo (mean DICE coefficient=0.48), chimpanzee–chimpanzee (mean=0.49), and bonobo–chimpanzee infant (mean=0.47) dyad groups indicated no significant differences for the DICE coefficients ($p=0.955$). We also found no significant effect when performing the same analyses for the mothers (mean values for bonobo–bonobo=0.47, chimpanzee–chimpanzee=0.34, bonobo–chimpanzee=0.38; $p=0.452$).

Discussion

We found no evidence to suggest that infants of the 2 *Pan* spp. shared gestures with their own or other mothers to any significant extent. This held true when we analyzed gestures from all contexts together and when we considered play gestures alone. In addition, gestures that were used more by mothers and unrelated adult females were less likely to be produced by infants (if at all) and vice versa. Gestural sharing among individuals of the same age group was, on the other hand, prevalent. Bonobo infants were homogeneous regarding the gestures they shared and again this held true when we restricted our analysis to the play context alone. In the same way bonobo mothers were homogeneous. We observed a similar tendency across species. Both bonobo and chimpanzee infants and bonobo and chimpanzee mothers performed similar types of gestures. However, in spite of the observed homogeneity of gesture types, infant and female adult peers (within and across species) demonstrated individual differences in the frequency that they used them.

The fact that infants and mothers shared few gestures indicates that vertical transmission through imitative learning can be excluded as the main mechanism at work in the gestural acquisition of *Pan* (Tomasello *et al.* 1989, 1994). This is further supported by recent theoretical suggestions that uniparental transmission of knowledge is an unlikely source for imitative learning within a group; instead it is far more feasible that a trait is established through monitoring multiple individuals (Enquist *et al.* 2010).

Interestingly, although play-related gestures were prominent in all age groups of *Pan* (ESM Table SI), the actual gesture types differed considerably between mother and infant. For example, almost all infant *Pan* (9 of 10) often used the *arm raise* signal to initiate play interactions but no adult female did. Even in a particular behavioral context such as play, infants and adults may pursue different communicative goals or use different gestures to achieve the same goal. Future research is needed to ascertain how age is implicated in the function of a gesture, e.g., when, how, and possibly why certain gestures are deprioritized, lost, or amalgamated with others.

Our findings contrast with previous reports that orangutans learn their gestures via uniparental imitative learning (Cartmill 2008). One explanation for this could be the different data gathering techniques (*ad libitum* vs. focal animal sampling) and operational definitions that were used. Alternatively, uniparental imitative learning may indeed be more important to infant orangutans (*cf.* Hirata and Celli 2003; Lonsdorf 2006). Compared with *Pan*, orangutan mother–infant dyads show a

prolonged intense relationship and therefore may encourage this form of knowledge transfer (Watts and Pusey 2002; Wich *et al.* 2004). Future research should compare the 2 genera using the same methods to clarify this.

Although we can only conjecture from the current data how the observation of peers might have influenced gestural acquisition and development, we suggest that horizontal transmission is unlikely to be responsible for the reported gestural overlap in bonobo infant and adult age groups. Three of 15 bonobo infant–infant dyads and 1 of 6 chimpanzee infant–infant dyads we investigated were housed in the same zoo group. Comparative *post hoc* analyses of these dyads with those in which members were housed in separate zoo groups revealed no marked differences in their relationship coefficients (Call and Tomasello 2007a). We found similar results for bonobo and chimpanzee mothers (ESM Table SII). Coupled with the fact that cross-species comparisons revealed no significant repertoire differences among infant and mother dyads, gestural similarity in the peer groups seems unlikely to have occurred solely through observing others.

The fact that bonobo infants (and mothers) shared a considerable number of gestures with peers (despite the majority of individuals being housed in different zoos), and the cross-species similarities observed in bonobos and chimpanzees suggests a substantial phylogenetic influence in gestural acquisition. *Pan* seems to have a biological predisposition to develop certain gestures in infancy (Genty *et al.* 2009; Hobaiter and Byrne 2011). However, it should also be noted that infants shared a common social context that may have guided gestural predispositions to develop in certain ways.

Despite the large overlap between gestural repertoires, we also observed variability. When comparing the similarity of gesture types, no dyad group exceeded a mean concordance coefficient of 0.62 (Table IV, DICE). Dyad members also demonstrated individual variability through the frequency that specific gestures were used. However, we are unable to draw any definitive conclusions about what caused this variability from the current study design. For example, gestural behavior is likely to be driven by individual preferences and motivations to varying extents, as well as differing opportunities for action, e.g., the availability of play partners.

Although a comparison of our findings with human gesturing would be informative, there are few studies that have systematically investigated how children learn their signals. However, within *Pan*, mothers may play a less active role in their offspring's gestural acquisition than human caregivers. Preverbal children seem to acquire at least some gestures via an imitation process that involves the caregiver, i.e., conventional gestures, such as hand waving to say goodbye (Liszkowski 2008; Masur 1980). Moreover, referential signals, such as *pointing*, are thought to emerge from a more deliberate social interaction such as communicative negotiation or a joint social activity with the caregiver (Bates *et al.* 1975; Bruner 1983; *cf.* Butterworth 2003).

Although this was the first systematic investigation of the gestural repertoires of mother–infant dyads of *Pan*, time and other resource limitations meant that sample sizes were small, particularly for chimpanzees. In addition, infants were the focal individuals under observation and we observed mothers only when they were in their offspring's close vicinity. However, the individual repertoire sizes we observed in bonobo and chimpanzee mothers were at least as high or comparable to the repertoire sizes reported in other studies using similar coding procedures (Pika *et al.* 2005a). We are therefore confident that although the mothers were not focal individuals, their repertoires at the time of observation were fully captured.

Although this study builds on our existing knowledge of gestural acquisition processes in nonhuman great apes, it has only scratched the surface in many ways. Beyond highlighting phylogenetic influences and the limited role that imitative learning from the mother plays in acquisition, we cannot unveil the full complexity of the underlying mechanisms involved. Single or multiple case study designs (Gomm *et al.* 2000) in which individuals are observed intensely and longitudinally in their early social interactions is crucial to trace the development of gestures and investigate the possible mechanisms underlying their emergence. Training studies in which mothers are instructed to use certain novel gestures could also produce useful data, although the application of this technique with nonhuman apes is not straightforward.

In conclusion, chimpanzee and bonobo infants did not appear to learn their gestures through imitating their mothers. Their early gestural repertoires seem to be forged by biological predisposition, and, we suggest, are shaped by social experiences encountered during life (Mason 1963; Rogers and Kaplan 2000). In-depth case studies could help us further unravel the complex relationship between the phylogenetic and ontogenetic influences implicated in gestural acquisition.

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