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5 **Title: What role do mothers play in the gestural acquisition of *Pan paniscus* and**

6 ***Pan troglodytes*?**

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9

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15

16   **Abstract**   Contemporary research hypothesizes that biological inheritance and

17   ontogenetic factors shape the development of gestural communication in nonhuman

18   great apes. Little is known, however, about the specific role that mothers play in the

19   acquisition of their infants' gestures. We observed six bonobo (*Pan paniscus*) and four

20   chimpanzee (*Pan troglodytes*) mother-infant dyads and recorded their gesture types and

21   frequency. We analyzed all behavioral contexts in which gestures occurred as well as

22   the play context alone. Infants of both species were unlikely to share gestures with their

23   mother or unrelated adult females. Gestural sharing was, however, prevalent within age

24   groups.   Within and across species, infant-infant and mother-mother groups were

25   homogenous regarding the types of gestures they shared; although there was individual

26   variation in the frequency of gesture use. Our findings provide limited evidence that

27   infants learned their gestures by imitating their mothers. Phylogenetic influences seem

28   to be vital in gestural acquisition but, we suggest, repertoire development cannot be

29   disentangled from individual social encounters during life.

30

31   **INTRODUCTION**

32   Currently, there is a lively debate about the relative importance of biological

33   inheritance and ontogenetic factors in the acquisition of gestural communication in

34   nonhuman great apes (e.g., Hobaiter and Byrne 2011; Liebal and Call 2011).   One

35   source of evidence supporting the biological inheritance of gestures comes through

36   observing young apes who developed species-typical gestures in the absence of role

37   models (i.e., they were unable to observe older conspecifics). Signals in these deprived

38   contexts, such as *chest beat* in gorillas (*Gorilla gorilla*), strongly resemble those

39   performed by conspecifics living in natural group compositions (Redshaw and Locke

40   1976). An alternative approach is to study more typically developing species groups.

41   For example, an analysis of captive and wild gorillas suggests that most of their gestures

42   belong to a *universal* species-typical pool and that apparent repertoire differences

43   between individuals and groups can be explained by varying ecological conditions

44   (Genty *et al.* 2009). 'Genetically channeled' gestural overlap has also been reported

45   across species. A recent study of wild chimpanzees (*Pan troglodytes*) found that

46   gestures were not only shared within community members, they were also comparable

47   with many gestures previously recognized across the three genera chimpanzees, gorillas

48   and orangutans (Hobaiter and Byrne 2011).

49   Evidence for the importance of ontogenetic influences in the gestural acquisition

50   process comes in the form of individual learning captured in a series of studies on

51   captive chimpanzee youngsters over a 12 year period (Tomasello *et al.* 1985, 1989,

52   1994, 1997).   Through a process of ontogenetic ritualization (described as

53   conventionalization by Smith 1977) a signal develops as two individuals shape each

54   other's behavior in repeated interactions (Tomasello and Call 1997).   A

55   noncommunicative behavior gains a communicative function through anticipation of the

56   socially interacting individuals over time. For example, a chimpanzee youngster slaps

57   her partner while playing. After several repetitions of this behavior the conspecific

58   recognizes the signal and anticipates the play behavior. The ritualization is complete

59   when the youngster raises its arm not to perform the physical act of slapping but to

60   demonstrate an abbreviated *arm raise* gesture to invite play (Tomasello and Call 1997).

61   Support for this process underpinning gestural acquisition comes from studies that have

62   witnessed the invention of new signals through social interactions and the highly

63   variable repertoires observed among individuals in species groups (Call and Tomasello

64   2007b).   Captive bonobos (*Pan paniscus*; Pika, Liebal and Tomasello 2005),

65   chimpanzees (Tomasello *et al.* 1985), gorillas (Pika *et al.* 2003); and orangutans (*Pongo*

66   *pygmaeus*; Liebal *et al.* 2006) all show idiosyncratic gestures, i.e., signals which are

67   performed by only one subject.

68   Gestures can also be acquired through imitative learning (see Zentall 2006).

69   Here individuals learn gestures by observing and subsequently replicating behaviors

70   from parents (vertical transmission), peers (horizontal transmission), or unrelated older

71   group members (oblique transmission; Cavalli-Sforza and Feldman 1981). Supporting

72   evidence is provided by group-specific gestures, i.e., gestures that are used by members

73   in one group but not in other groups. For example, Liebal *et al.* (2006) observed the

74   signal *offer arm with food pieces* in a single group of captive orangutans (for similar

75   observations in captive gorillas and bonobos, see Pika *et al.* 2003; Pika, Liebal and

76   Tomasello 2005).

77   Study of the mother-infant relationship is likely to elucidate important

78   information about the origin of gestures. All great apes have extended periods of

79   immaturity (Pereira and Fairbanks 2002), and, hence, the mother-infant dyad is

80   characterized by a long-lasting, and intense relationship (Hoff *et al.* 1981; Plooij 1978,

81   1984; van Lawick-Goodall 1967). In orangutans and chimpanzees, for example, the

82   mother plays an important role in the development and facilitation of foraging skills

83   (Bard 1992; Hirata and Celli 2003; Jaeggi *et al.* 2010; Lonsdorf 2006; van Schaik

84   2004). Mothers are also the most important social partner when infants begin to gesture

85   (which is broadly speaking between 1 and 1.5 years of life in nonhuman great apes;

86   Plooij 1978; Schneider *et al.* 2011) and are essential during an infant's socialization

87   process (King 2004; Maestripieri and Call 1996).

88   Gestural research has, however, neglected the mother-infant dyad context. In the

89   only systematic investigation of the mechanisms underlying gestural acquisition,

90   Cartmill (2008) compared repertoire overlaps among eight orangutan youngsters (seven

91   aged 10 – 25 months, and one aged 30 – 48 months) and their mothers (including two

92   foster, i.e., nonbiological, mothers). The association between infant and caregiver was

93   important to the imitative learning of gestures. Infants shared more gestures with their

94   mother or adoptive mother than they did with other adult female group members. This

95   is in contrast to chimpanzees where peers seemed to be more important than the mother

96   in gestural development (Tomasello *et al.* 1989, 1994).

97   Our objective in the present study was to investigate more directly the role

98   played by mothers in the gestural development of their infants. We used an

99   observational method to contrast, within and between *Pan* species (bonobo and

100   chimpanzee), the following dyads: infant-(biological) mother, infant-unrelated adult

101   female, infant-infant, and mother-mother. For each dyad observed, we recorded and

102   compared the types of gestures exhibited and their frequency. This allowed us to

103   address the following three issues.   First, we explored the role that bonobo and

104   chimpanzee mothers played in their infants' gestural acquisition by examining the

105   extent that gestures were shared.   A significant overlap within this dyad would

106   emphasize the importance of imitative learning in gestural acquisition.   Second, we

107   investigated the extent that peers (infant and mother age group) shared gestures within

108   and across the two *Pan* species.   Age group overlap across species would signify the

109   importance of phylogenetic influences in the gestural acquisition process.   Third, we

110   examined the gesture frequency for all dyads observed in order to capture individual

111   variability and the importance of social encounters in early life.

METHODS

Subjects

114   We observed six bonobo (*Pan paniscus*) and four chimpanzee (*Pan troglodytes*)

115   infants in their first 20 months of life (Table 1).   All infants were born in captivity, lived

116   in socially housed groups in six European zoos, and were raised by their biological

117   mothers.   The group sizes ranged between five and eight individuals in bonobos and

118   between 11 and 20 individuals in chimpanzees (for details of the age composition of

119   each group see Table 1).

120   ------------
121   TABLE 1
122   ------------

Observational and coding procedure

124   The first author and research assistants videotaped the observations between July

125   2005 and August 2008.   We used focal animal sampling to record the infants' social

126   interactions (Altmann 1974).   We observed each infant either once every week or twice

127   every second week, which resulted in four sessions (each lasting 15 minutes) and one

128   hour of video footage per subject per month.   The time of the observations varied

129   between 8:30 a.m. and 7 p.m., with sessions for every subject distributed across the

130   apes' diurnal activity.   We observed each infant for a period of between six and 19

131   months during their first 20 months of life (Table 1).   Overall, we recorded bonobos for

132   67 hours and chimpanzees for 55 hours.   We incorporated a subset of coded data (which

133   accounted for one third of the whole dataset) from a research project investigating

134   gestural onset and early use in nonhuman great apes (Schneider *et al.* 2011).

135   A gesture was defined as a motoric action (perfomed by head, limbs, or whole

136   body) that fulfilled the following criteria: 1) it was directed to a particular recipient

137   (accompanied by orienting body towards recipient and gazing at them; adopted from

138   Call and Tomasello 2007b; Wetherby *et al.* 1988); 2) it served a functional purpose

139   (Call and Tomasello 2007b); and 3) the sender needed to show anticipation of

140   recipients' reaction accompanied by gazing (Bates *et al.* 1975; Bruner 1981; Tomasello

141   *et al.* 1994).   This definition excludes simple mechanical actions produced to achieve a

142   desired outcome without leaving the recipient the choice of action, e.g., to relocate

143   another individual by applying physical force (Call and Tomasello 2007b).   Gestures

144   could be tactile, visual, or auditory (see below).

145   We recorded all gestures produced by the focal animals (directed to mother or

146   other group members) and their mothers (directed to the infant or other group

147   members).   Mothers' gestures were noted whenever they were near the infant and

148   therefore in view of the camera.   To ensure that comprehensive repertoires were

149   captured for the mothers (who were not focal animals), we analyzed, where available,

150   additional video footage of their gestural behavior prior to the infants' first gestures (on

151   average infants in the current sample started gesturing at 11 months). For each gesture

152   we coded the following variables: sender and recipient, sex and age group (0 − 2.5

153   years, 2.6 − 5 years, 6 − 9 years, ≥ 10 years), gesture modality (tactile: signal was

154   transferred by initiating body contact with recipient; visual: signal was transferred over

155   a distance via particular body movements or postures; auditory: signal was transferred

156   via the acoustic channel but was nonvocal), gesture type, and behavioral context as

157   judged by the available pre- and post information that accompanied the senders' signal

158   (see electronic supplementary material, Table S1 for behavioral descriptions of gesture

159   types and contexts).

160   **Interobserver reliability**

161   The first author (CS) coded all video footage. To determine reliability a naïve

162   second person coded 20% of randomly chosen infant and mother gestures. We used

163   Cohen's Kappa to measure the degree of concordance between raters for gesture type

164   and behavioral context (Altman 1991). Kappa could not, however, be computed when

165   we identified unbalanced coding between raters, resulting in asymmetry in the table,

166   e.g., one rater used codes 1 − 3, whereas the other rater never used 1 at all. Here, we

167   used a permutation procedure to determine the coefficient (Manly 1997; software

168   written by R. Mundry). First, the original agreement between the two observers was

169   established. The codes of one observer were then randomized and the agreement was

170   measured again. In total 1,000 randomizations were conducted (with the original data

171   included as one permutation). Afterwards the original agreement was compared with

172   the distribution of agreements derived from the permutations. The P-value was

173   determined by the proportion of permutations that showed agreement at least as large as

174   the original data. The Kappa coefficient was determined as usual [$K =$ (observed

175   agreement - expected agreement) / (1 - expected agreement)], whereby the expected

176   agreement was the average agreement revealed from truly permuted data. By applying

177   this procedure, we retained the information from every observation and ensured that

178   Kappa was an appropriate measure of the reliability of the original codes. For the

179   gesture types the Kappa values ranged between 0.76 (mother) and 0.82 (infant), and

180   0.73 (mother) and 0.73 (infant) for the behavioral contexts. All Kappa values were

181   highly significant ($P < 0.002$), and according to Altman (1991) equated to a 'good' or

182   'very good' level of agreement.

Data analyses and statistics

184   We applied the Kendall rank correlation coefficient Tau (τ) to correlate the

185   frequencies with which distinct gestures occurred in two individuals of a given dyad.

186   We determined the correlation twice per dyad; once based on only those gestures shown

187   by both individuals (*only both* dataset) and once including each gesture shown by at

188   least one of the two individuals, i.e., their entire repertoires (*at least once* dataset). A τ

189   of -1 indicates that gestures frequently performed by one individual were never shown

190   by the other individual, whereas a τ of +1 indicates that relative frequencies by which

191   the two individuals exhibited the gestures were in perfect agreement. We calculated the

192   DICE-coefficient C_D (Dice 1945) to obtain a measure of how similar the repertoires of

193   two individuals were [with C_D = 2 x number of gestures common for subject A and B /

194   (total number of gestures shown by subject A + total number of gestures shown by

195   subject B)]. This coefficient indicates the proportion of shared gestures used in a dyad

196   and ranges between 0 and 1; 0 indicates that two individuals did not share any gesture

197   and 1 indicates a perfect match of gesture repertoires in a dyad.

198   In the case of the correlation datasets (*only both* and *at least once)*, we applied

199   Fisher's omnibus tests (Haccou and Meelis 1994) to ascertain whether single significant

200   *P*-values were spurious.   Here the *P*-values of the correlation coefficients were

201   integrated into a single χ^2-distribution, where the degrees of freedom were twice the

202   number of *P*-values incorporated.   We then tested whether correlations between

203   frequencies of gestures differed among dyad-types (infant-own mother *or* infant-other

204   mothers) as well as among species.   To do so, we undertook a repeated-measures

205   ANOVA for the proportions of shared gestures (DICE) and for each correlation dataset

206   (*only both* and *at least once*), into which we included species as a between-subjects

207   factor and dyad-type as a within-subjects factor.

208   Next, we compared the similarities between repertoires among different groups

209   of dyads (DICE-coefficients of shared gestures and correlations between gesture

210   frequencies).   First, we conducted comparisons between infant-infant, mother-mother,

211   and infant-mother (own and other) dyads. We considered only bonobos for this analysis

212   as they were the only species with a large enough sample size.   If such a test is

213   significant it could, for instance, indicate that repertoires of infants are particularly

214   homogeneous (i.e., show larger similarity with one another rather than with mothers, or

215   mothers with one another).   Second, we compared bonobo-bonobo, chimpanzee-

216   chimpanzee, and bonobo-chimpanzee dyads.   Last, we repeated this comparison for

217   mothers (bonobo-bonobo, chimpanzee-chimpanzee, and bonobo-chimpanzee).   These

218   three analyses could not be carried out using standard tests since the data were not

219   independent (i.e., each individual was involved in several dyadic measures of

220   similarity).   Hence, we used a permutation test (Adams and Anthony 1996; Manly

221   1997), similar to a Mantel-test for matrix correlation (Sokal and Rohlf 1995).   In the

222   present analysis, one matrix denoted the dyadic similarity (e.g., the correlation between

223   frequencies by which gestures occurred in the two subjects of a dyad); the other matrix

224   represented the dyad-type (e.g., infant-mother, mother-mother, etc.). The test statistic

225   consisted of the sum of the squared differences between mean similarity measures per

226   dyad-type and the mean similarity measures of all dyads. Permutations were achieved

227   by simultaneously randomizing rows and columns of one of the two matrices. By

228   conducting 1,000 permutations (into which the original data was included as one

229   permutation) the sampling distribution of the test statistic was obtained under the

230   assumption of a true null hypothesis. Finally, the *P*-value was estimated as the

231   proportion of test statistics in the sampling distribution being at least as large as that of

232   the original data.

233   We calculated the repeated-measures ANOVAs using SPSS 15.0. We computed

234   the Fisher's omnibus test by hand, and for the matrix permutation test, we used a script

235   (written by R. Mundry) for R 2.9.1 (R Development Core Team 2009).

236

RESULTS

Description of mother-infant gestural repertoires

We analyzed a total of 1,269 gestures (comprising 39 distinct gesture types). The six bonobo infants produced 247 gestures (consisting of 21 types) and their mothers 561 gestures (26 types). The four chimpanzee infants employed 184 gestures (25 types) and their mothers 277 gestures (22 types; see electronic supplementary material, Table S1 for signal types observed and corresponding sensory domain in infants and mothers of each species).

Infant repertoires ranged from five to 17 gesture types in bonobos and from ten to 17 gesture types in chimpanzees. Mother repertoires consisted of 11 to 18 gesture types in bonobos and nine to 14 in chimpanzees (Table 2).

TABLE 2

Similarity of repertoires within mother-infant dyads

Overall, *P*-values derived from the Kendall correlation coefficients (Table 3) 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 at least one dyad member (*at least once* dataset). The coefficients ranged from 0.01 to -0.58 (infant-own mother) and -0.14 to -0.54 (infant-other mothers); the 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 3). The correlations for gestures that were employed by both members of

261   a dyad (*only both* dataset), however, were nonsignificant in infant-own mother dyads

262   (Fisher's omnibus test: $\chi^2 = 14.79$, *df* = 18, *P* = 0.676) and infant-other mothers dyads

263   ($\chi^2 = 9.32$, *df* = 20, *P* = 0.979; Table 3).   Here, the corresponding coefficients ranged

264   from 0.33 to -1.00 (infant-own mother) and 0.38 to -0.61 (infant-other mothers).

265   ------------
266   TABLE 3
267   ------------

268   A repeated-measures ANOVA on each correlation dataset (*only both* and *at least*

269   *once*) with the factors species (bonobo versus chimpanzee) and type of dyad (infant-

270   own mother versus infant-other mothers), indicated no differences between bonobo and

271   chimpanzees (*only both*: $F(1,7) = .022$, *P* = 0.887; *at least once*: $F(1,8) = .069$, *P* =

272   0.800), or dyad-type (*only both*: $F(1,7) = .459$, *P* = 0.520; *at least once*: $F(1,8) = 1.137$,

273   *P* = 0.317).   We found no significant interaction between these factors (*only both*:

274   $F(1,7) = 2.29$, *P* = 0.174; *at least once*: $F(1,8) = .202$, *P* = 0.665).   Infants of both

275   species showed a similar frequency of gesture occurrences (concerning gestures that

276   occurred in both individuals or in at least one dyad-member) with unrelated adult

277   females as they did with their own mothers (Table 3).   A further repeated-measures

278   ANOVA on the proportions of shared gestures, with the factors species (bonobo versus

279   chimpanzee) and type of dyad (infant-own mother versus infant-other mothers), also

280   indicated no difference between bonobos and chimpanzees ($F(1,8) = 1.009$, *P* = 0.345),

281   or dyad-types ($F(1,8) = .430$, *P* = 0.530).   Again, we found no significant interaction

282   between these factors ($F(1,8) = .493$, *P* = 0.503).

283   **Further comparison of dyad-groups**

284   Permutation analysis revealed no significant differences in frequency of

285   occurrence of gestures for both individuals of a dyad in bonobos (*P* = 0.221;

286   correlations based on *only both* data). However, the comparison of repertoires yielded a

287   significant overall effect when analyzing proportions of shared gestures in a dyad (P =

288   0.001; Fig. 1a), as well as the correlations between frequencies of gestures which were

289   shown by at least one of two dyad-members (P = 0.004; Fig. 1b). Post hoc tests

290   revealed that the homogeneity in terms of shared gestures and gesture frequency in the

291   infant-infant group differed significantly from that in the infant-mother group (DICE: P

292   = 0.001; *at least once*: P = 0.003). Likewise, the mother-mother group differed in their

293   homogeneity from that of the infant-mother group for each dataset (DICE: P = 0.001; *at*

294   *least once*: P = 0.008). The infant-infant and mother-mother groups, however, did not

295   differ significantly from each other (DICE: P = 0.649; *at least once*: P = 0.171). For

296   both datasets therefore, infant-infant and mother-mother dyads showed more

297   homogeneity than mother-infant dyads. We observed a similar pattern in chimpanzees

298   (Fig. 2) but due to the small sample size a test of significance was not possible.

299   ------------- -------------
300   FIGURE 1   FIGURE 2
301   ------------- , -------------
302   Comparisons of the bonobo-bonobo, chimpanzee-chimpanzee, and bonobo-

303   chimpanzee infant dyad-groups indicated no significant differences for any of the three

304   datasets (*only both*: P = 0.256; *at least once*: P = 0.194; DICE: P = 0.189; Table 4).

305   The shared types and frequencies of gestures for bonobo and chimpanzee infants did not

306   differ significantly between the three groups, i.e., neither of the two species were more

307   homogeneous than the other or the between species dyads. We found no indication of a

308   significant effect when performing the same analyses for mothers (*only both*: P = 0.416;

309   *at least once*: P = 0.956; DICE: P = 0.911; Table 4).

310   ------------
311   TABLE 4
312   ------------

313   **Focusing on play-related gestures**

314   To ascertain whether the observed gestural similarities and dissimilarities

315   depended on behavioral context we analyzed gesture use by context (e.g., play,

316   ingestion; see electronic supplementary material, Table S1). However, in doing so the

317   numbers of gestures available for analysis decreased considerably and play was the only

318   context in which there was a sufficient amount across species and age groups to allow

319   meaningful analysis. We restricted the analyses to the proportions of shared gestures

320   (DICE) for the same reason and no longer conducted frequency analyses. Following the

321   calculations of the DICE-coefficients we carried out a repeated-measures ANOVA and

322   permutation tests in the same way as we did with the overall dataset (see above).

323   Overall, we observed 498 play-related gestures (comprising 30 gesture types).

324   The 10 infants produced 246 play gestures (24 types) and their mothers 252 (17 types;

325   see electronic supplementary material, Table S1 for number of gestures observed in play

326   in infants and mothers of each species). Bonobo infants used between four and 13

327   gesture types, and chimpanzee infants between six and 11 types. Bonobo mothers

328   showed between four and 10 gesture types, while chimpanzee mothers used between

329   one and eight. Of the four chimpanzee mother-infant dyads, only a single dyad shared

330   any gestures (two types) with each other. In bonobos, four of six mother-infant dyads

331   shared gestures (between one and five types per dyad).

332   A repeated-measures ANOVA with the factors *species* and *dyad-type* (infant-

333   own mother versus infant-other mothers) showed no difference between species ($F(1,8)$

334   = 2.226, P = 0.174) or dyad-types ($F(1,8)$ = .207, P = 0.661), and no significant

335   interaction between factors ($F(1,8)$ = .719, P = 0.421). Infants of both species shared a

336   similarly low number of gestures with unrelated adult females (mean DICE-coefficients;

337   bonobo = 0.21, *N* = 6; chimpanzee = 0.14, *N* = 4) as they did with their own mothers

338   (bonobo = 0.23, chimpanzee = 0.07).

339   When comparing shared play-related gestures exhibited in dyad-groups (infant-

340   infant, mother-mother, and infant-mother), we found a significant overall effect for

341   bonobos (*P* = 0.001; Fig. 3a). Post hoc permutation tests revealed that the homogeneity

342   in terms of shared play gestures in the infant-infant group differed significantly from

343   that in the infant-mother group (*P* = 0.001).   Likewise, the mother-mother group

344   differed in their homogeneity from that of the infant-mother group (*P* = 0.001).   The

345   infant-infant and mother-mother groups, however, did not differ significantly from each

346   other (*P* = 0.917). Conclusively, infant-infant and mother-mother dyads showed more

347   homogeneity than mother-infant dyads (see Fig. 3b for chimpanzees).

348   -------------
349   FIGURE 3
350   -------------

351   Comparisons of bonobo-bonobo (mean DICE-coefficient = 0.48), chimpanzee-

352   chimpanzee (mean = 0.49), and bonobo-chimpanzee infant (mean = 0.47) dyad-groups

353   indicated no significant differences for the DICE-coefficients (*P* = 0.955). We also

354   found no significant effect when performing the same analyses for the mothers (mean

355   values for bonobo-bonobo = 0.47, chimpanzee-chimpanzee = 0.34, bonobo-chimpanzee

356   = 0.38; *P* = 0.452).

357   **DISCUSSION**

358   We found no evidence to suggest that infants of the two *Pan* species shared

359   gestures with their own or other mothers to any significant extent. This held true when

360   we analyzed gestures from all contexts together and when we considered play gestures

361   alone. In addition, gestures that were used more by mothers and unrelated adult females

362   were less likely to be produced by infants (if at all) and vice versa. Gestural sharing

363   among individuals of the same age group was, on the other hand, prevalent. Bonobo

364   infants were homogenous regarding the gestures they shared and again this held true

365   when we restricted our analysis to the play context alone. In the same way bonobo

366   mothers were homogenous. We observed a similar tendency across species. Both

367   bonobo and chimpanzee infants and bonobo and chimpanzee mothers performed similar

368   types of gestures. However, in spite of the observed homogeneity of gesture types,

369   infant and female adult peers (within and across species) demonstrated individual

370   differences in the frequency that they used them.

371   The fact that infants and mothers shared few gestures indicates that vertical

372   transmission through imitative learning can be excluded as the main mechanism at work

373   in the gestural acquisition of *Pan* (see also Tomasello *et al.* 1989, 1994). This is further

374   supported by recent theoretical suggestions that uniparental transmission of knowledge

375   is an unlikely source for imitative learning within a group; instead it is far more feasible

376   that a trait is established through monitoring multiple individuals (Enquist *et al.* 2010).

377   Interestingly, while play-related gestures were prominent in all age groups of

378   *Pan* (see electronic supplementary material, Table S1), the actual gesture types differed

379   considerably between mother and infant. The *arm raise* signal, for example, was often

380   used to initiate play interactions by almost all *Pan* infants (nine of ten), but no adult

381   female did. Even in a particular behavioral context such as play, infants and adults may

382   pursue different communicative goals or use different gestures to achieve the same goal.

383   Future research is needed to ascertain how age is implicated in the function of a gesture,

384   e.g., when, how and possibly why certain gestures are de-prioritized, lost or are

385   amalgamated with others.

386   Our findings contrast with previous reports that orangutans learn their gestures

387   via uniparental imitative learning (Cartmill 2008). One explanation for this could be the

388   different data gathering techniques (ad libitum versus focal animal sampling) and

389   operational definitions that were used. Alternatively, uniparental imitative learning may

390   indeed be more important to infant orangutans (cf., Hirata and Celli 2003; Lonsdorf

391   2006). Compared with *Pan,* orangutan mother-infant dyads show a prolonged intense

392   relationship and therefore may encourage this form of knowledge transfer (Watts and

393   Pusey 2002; Wich *et al.* 2004). Future research should compare the two species using

394   the same methods to clarify this.

395   Although we can only conjecture from the current data how the observation of

396   peers might have influenced gestural acquisition and development, we suggest that

397   horizontal transmission is unlikely to be responsible for the reported gestural overlap in

398   bonobo infant and adult age groups. Three of 15 bonobo infant-infant dyads and one of

399   six chimpanzee infant-infant dyads we investigated were housed in the same zoo group.

400   Comparative post hoc analyses of these dyads with those where members were housed

401   in separate zoo groups revealed no marked differences in their relationship-coefficients

402   (see also Call and Tomasello 2007a). We found similar results for bonobo and

403   chimpanzee mothers (see electronic supplementary material, Table S2). Coupled with

404   the fact that cross-species comparisons revealed no significant repertoire differences

405   among infant and mother dyads, gestural similarity in the peer groups seems unlikely to

406   have occurred solely through observing others.

407   The fact that bonobo infants (and mothers) shared a considerable number of

408   gestures with peers (despite the majority of individuals being housed in different zoos),

409   and the cross-species similarities observed in bonobos and chimpanzees, suggests a

410   substantial phylogenetic influence in gestural acquisition. *Pan* seems to have a

411   biological predisposition to develop certain gestures in infancy (see Genty *et al.* 2009;

412   Hobaiter and Byrne 2011). However, it should also be noted that infants shared a

413   common social context that may have guided gestural predispositions to develop in

414   certain ways.

415   Despite the large overlap between gestural repertoires, we also observed

416   variability. When comparing the similarity of gesture types, no dyad-group exceeded a

417   mean concordance coefficient of 0.62 (see Table 4, DICE). Dyad members also

418   demonstrated individual variability through the frequency that specific gestures were

419   used. However, we are unable to draw any definitive conclusions about what caused

420   this variability from the current study design. For example, gestural behavior is likely

421   to be driven by individual preferences and motivations to varying extents, as well as

422   differing opportunities for action, e.g., the availability of play partners.

423   Although a comparison of our findings with human gesturing would be

424   informative, there are few studies that have systematically investigated how children

425   learn their signals. *Pan* mothers may, however, play a less active role in their

426   offspring's gestural acquisition than human caregivers. Preverbal children seem to

427   acquire at least some gestures via an imitation process that involves the caregiver (i.e.,

428   conventional gestures, such as hand waving to say goodbye; e.g., Liszkowski 2008;

429   Masur 1980). Moreover, referential signals, such as *pointing,* are thought to emerge

430   from a more deliberate social interaction such as communicative negotiation or a joint

431   social activity with the caregiver (e.g., Bates *et al.* 1975; Bruner 1983; cf., Butterworth

432   2003).

433   While this was the first systematic investigation of the gestural repertoires of

434   *Pan* mother-infant dyads, time and other resource limitations meant that sample sizes

435   were small, particularly for chimpanzees. In addition, infants were the focal animal

436   under observation and we observed mothers only when they were in their offspring's

437   close vicinity. However, the individual repertoire sizes we observed in bonobo and

438   chimpanzee mothers were at least as high or comparable to the repertoire sizes reported

439   in other studies using similar coding procedures (Pika, Liebal, Call and Tomasello

440   2005). We are therefore confident that although the mothers were not focal animals,

441   their repertoires at the time of observation were fully captured.

442   While this study builds on our existing knowledge of gestural acquisition

443   processes in nonhuman great apes, it has only scratched the surface in many ways.

444   Beyond highlighting phylogenetic influences and the limited role that imitative learning

445   from the mother plays in acquisition, we cannot unveil the full complexity of the

446   underlying mechanisms involved. Single or multiple case study designs (Gomm *et al.*

447   2000) where individuals are observed intensely and longitudinally in their early social

448   interactions is crucial to trace the development of gestures and investigate the possible

449   mechanisms underlying their emergence. Training studies in which mothers are

450   instructed to use certain novel gestures could also produce useful data, although the

451   application of this technique with nonhuman apes is not straightforward.

452   In conclusion, chimpanzee and bonobo infants did not appear to learn their

453   gestures through imitating their mothers. Their early gestural repertoires seem to be

454   forged by biological predisposition, and, we suggest, are shaped by social experiences

455   encountered during life (see Mason 1963; Rogers and Kaplan 2000). In-depth case

456   studies could help us further unravel the complex relationship between the phylogenetic

457   and ontogenetic influences implicated in gestural acquisition.

458

467

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Table 1. Details of the study subjects (size and age distribution of group was determined at infant's birth).

Species	*Infant*	*Sex*	*Date of Birth*	*Size and age distribution of group* [A = adult (≥ 10 years); S = subadult (6–9 years); J = juvenile (2.6–5 years); I = infant (0–2.5 years)]	*Observation regularity*	*Observation period* (age in months)	*Total observation time in hours*	*Location*
Bonobo	Habari	Male	29/01/06	8 (5A, 1S, 2I[b])	Biweekly	13 – 20	8	Mechelen
	Hongo	Male	25/02/06	8 (5A, 1S, 1I + 1I[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
	Nayembi	Female	26/04/06	8 (4A, 2S, 2J)	Biweekly	12 – 19	8	Apeldoorn
Chimpanzee	Gihneau	Male	29/12/05	20 (16A, 3S, 1I)	Biweekly	14 – 19	6	Arnhem
	Kara	Female	23/06/05	17 (9A, 2S, 3J + 1J[a], 1I + 1I[b])	Weekly	2 – 20	19	Leipzig
	Kofi	Male	07/07/05	17 (9A, 2S, 3J + 1J[a], 2I)	Weekly	2 – 20	19	Leipzig
	Nafia	Female	10/06/06	11 (6A, 3S, 2I)	Weekly	10 – 20	11	Münster

[a] Left group during study. [b] Born during study.

Table 2. 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	Djanoa-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

Table 3. Kendall rank correlation coefficients (T) and corresponding *P*-values between infant-own mother and infant-other mothers.

| | | At least once *dataset* | | | | Only both *dataset* | | | |
| | | Own mother | | Other mothers[a] | | Own mother | | Other mothers[a] | |
Species	Infant	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 one gesture with his mother. He was therefore excluded from all *only both* analyses as a coefficient could not be calculated.

Table 4. Mean coefficient values for *only both*- and *at least once*-correlations and DICE dataset.

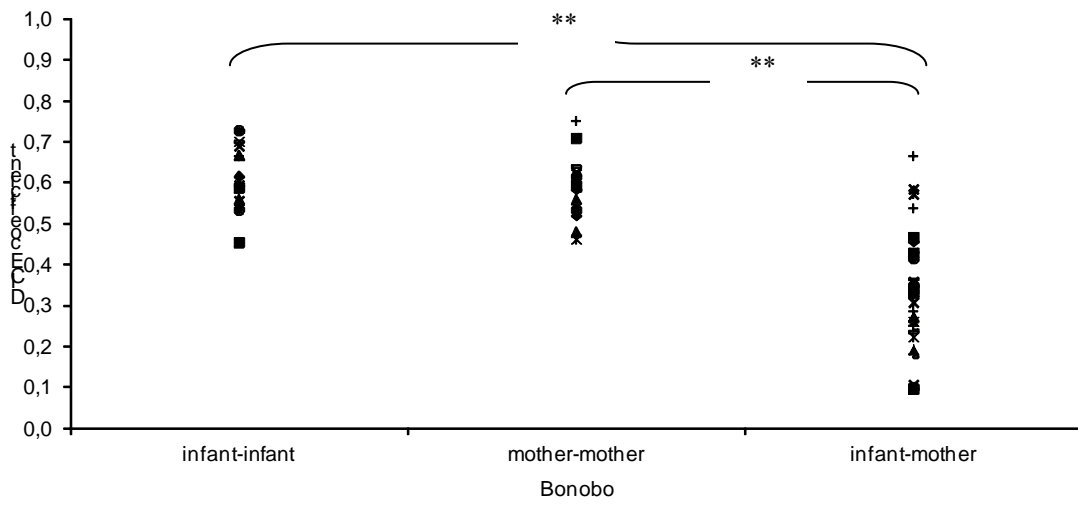| | *Dataset* | *Species comparison* | | |
		Bonobo-Bonobo	*Chimpanzee-Chimpanzee*	*Bonobo-Chimpanzee*
Infants	Only both (Tau)	0.09	0.38	0.09
	At least once (Tau)	0.22	0.03	0.14
	DICE C_D	0.62	0.54	0.58
Mothers	Only both (Tau)	0.20	0.05	0.28
	At least once (Tau)	0.04	0.02	0.05
	DICE C_D	0.59	0.57	0.59

FIGURE LEGENDS

Figure 1. Repertoire similarities for bonobos in the three dyad-groups infant-infant (N = 15), mother-mother (N = 15) and infant-mother (N = 36). (a) DICE-coefficients and (b) coefficients of *at least once* dataset.

Figure 2. Repertoire similarities for chimpanzees among infant-infant (N = 6), mother-mother (N = 6) and infant-mother dyads (N = 16). (a) DICE-coefficients and (b) coefficients of *at least once* dataset.

Figure 3. Similarities of play gestures (DICE-coefficients) for (a) bonobos in the three 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).
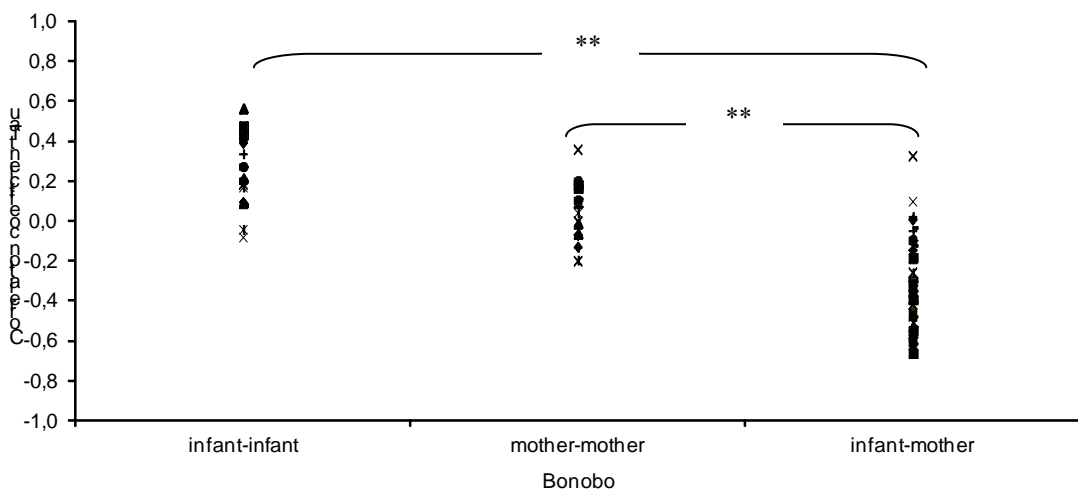
FIGURES

(a)

(b)

Figure 1. Repertoire similarities for bonobos in the three dyad-groups infant-infant (*N* = 15), mother-mother (*N* = 15) and infant-mother (*N* = 36). (a) DICE-coefficients and (b) coefficients of *at least once* dataset.
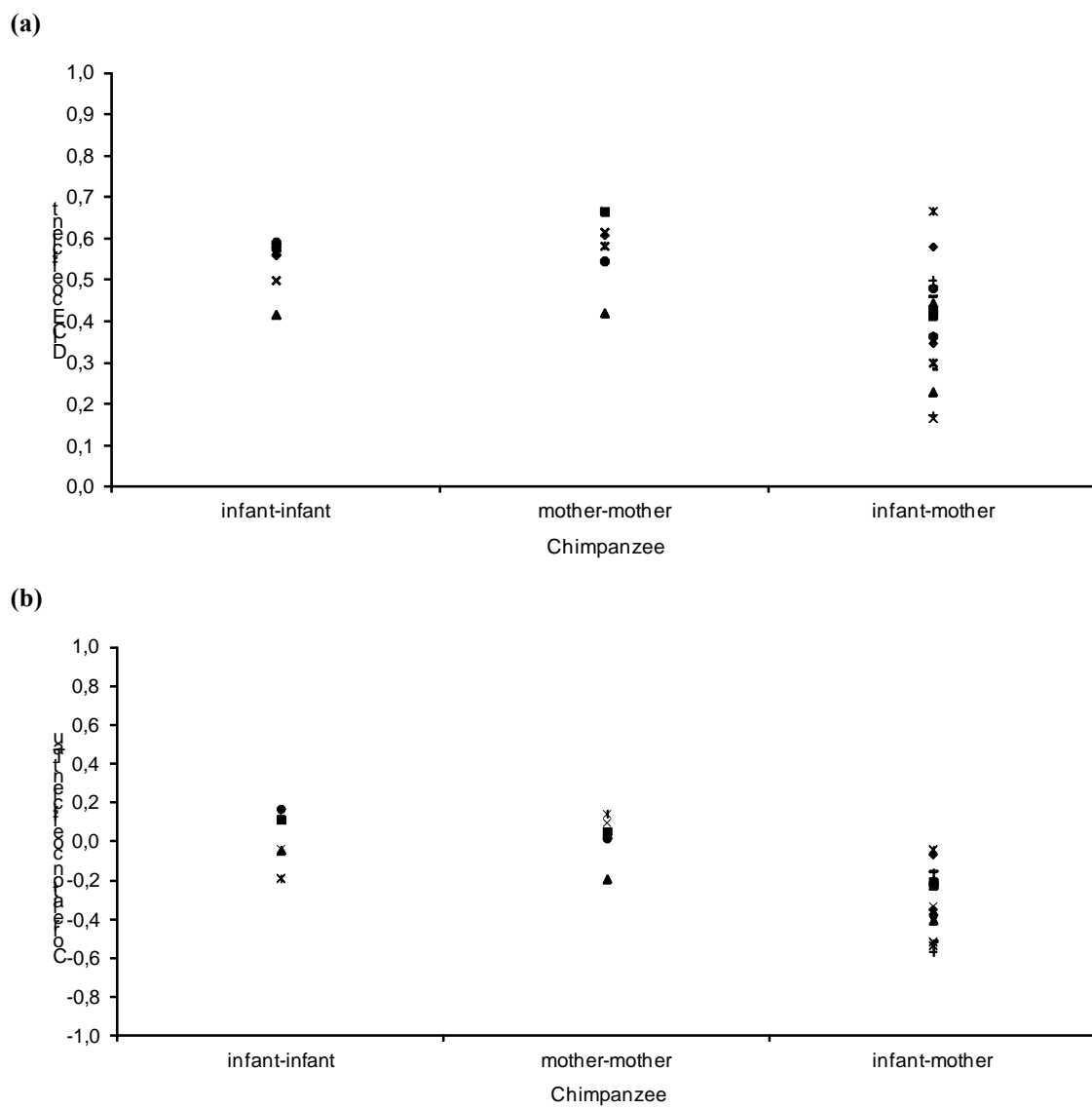
(a)

(b)

Figure 2. Repertoire similarities for chimpanzees among infant-infant (*N* = 6), mother-mother (*N* = 6) and infant-mother dyads (*N* = 16). (a) DICE-coefficients and (b) coefficients of *at least once* dataset.
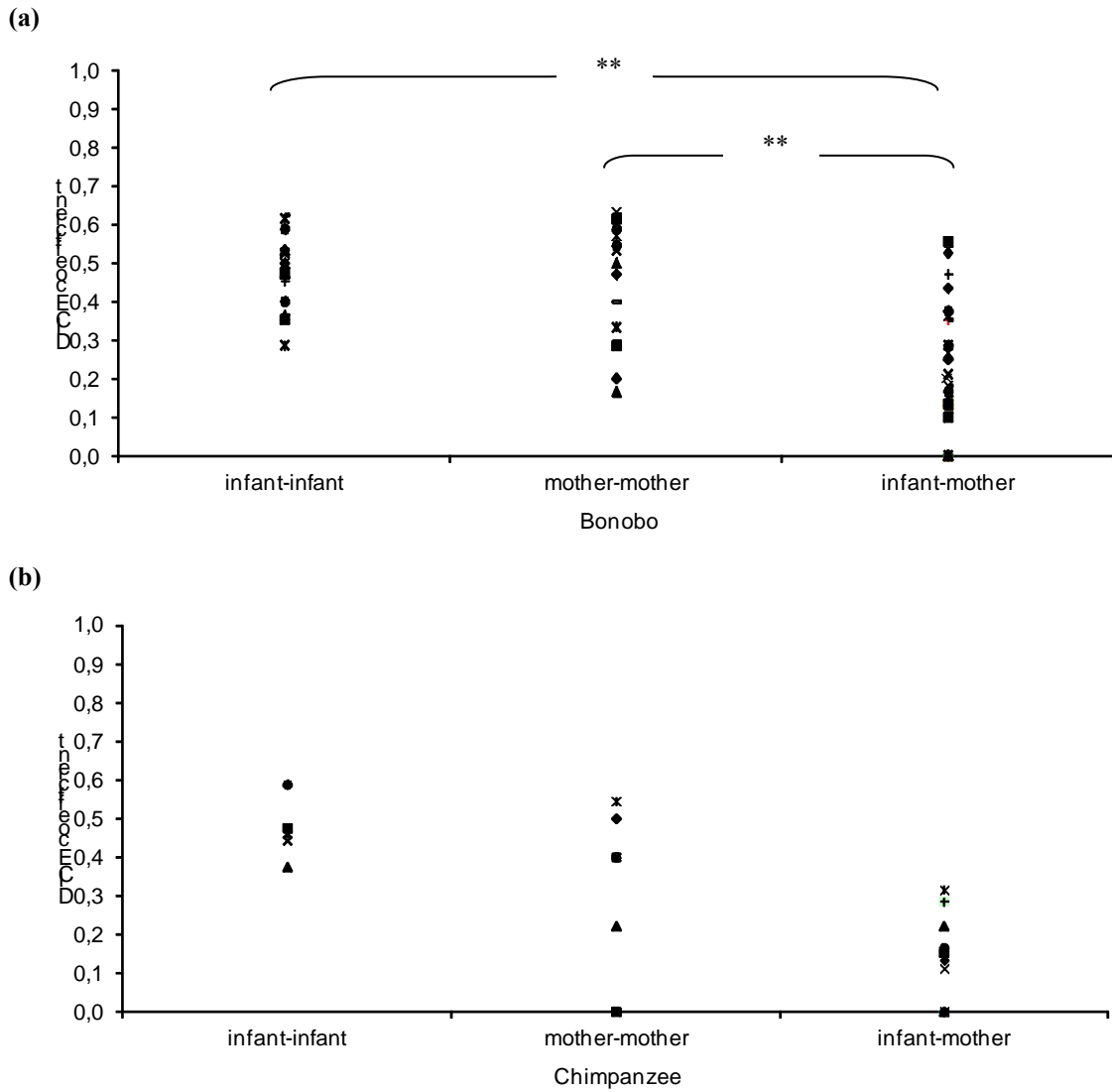
(a)

(b)

Figure 3. Similarities of play gestures (DICE-coefficients) for (a) bonobos in the three 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).

ELECTRONIC SUPPLEMENTARY MATERIAL

Table S1. Gesture types, sensory modality and behavioral contexts observed in genus *Pan* infants and mothers (numbers in parenthesis reflect the total number of occurrences, numbers without parenthesis represent the number of gesture types).

Coding category	Associated subcategories	Description	Bonobo (N = 6)		Chimpanzee (N = 4)	
			Infant	*Mother*	*Infant*	*Mother*
Modality & Gesture type						
Tactile	Arm on	Finger(s), hand(s) or arm(s) were placed on any body part of the recipient; possibly holding on to recipients' body	✓ (16)	✓ (76)	✓ (15)	✓ (49)
	Body beat	Repeated, consecutive hits (see 'hit' description) executed with the same body part (i.e., hand(s), arm(s) or foot/feet)	✓ (20)	✓ (2)	✓ (4)	
	Formal bite	Gentle bite of recipients' body	✓ (2)	✓ (73)	✓ (2)	✓ (68)
	Gentle touch	Very gentle touch or hold of recipients' body with finger(s) or hand(s)		✓ (3)	✓ (1)	✓ (4)
	Hit	Single and forceful hit of recipients' body with hand(s), arm(s) or foot/feet	✓ (38)	✓ (3)	✓ (27)	✓ (3)
	Hold chin	Place hand around chin of recipient and hold		✓ (9)		✓ (1)
	Lead	Place hand or arm around a body part (e.g., the neck) of the recipient and lead them in a certain direction		✓ (14)		✓ (5)
	Lip-lip touch	Touch recipients' mouth with one's own mouth	✓ (2)		✓ (2)	✓ (4)
	Nudge	Brief movement towards recipients' body with single finger(s), hand, or foot; also kind of pinch		✓ (52)	✓ (3)	✓ (59)
	Pull	Grasp a part of recipients' body with hand or foot and perform a short (+/- forceful) movement	✓ (1)	✓ (20)		✓ (5)
	Push	Exert pressure on recipients' body with hand(s), arm(s) or foot/feet		✓ (51)	✓ (2)	✓ (10)
	Push with object	Poke or hit recipient with an object		✓ (4)		✓ (3)
	Rest head	Place one's own head on recipients' body			✓ (3)	
	Shake body	Shake a part (e.g., head, arm) or body of recipient (e.g., infant)		✓ (7)		✓ (3)
	Tap	Tap or poke with knuckle(s), single finger(s) or whole hand repeatedly on recipients' body	✓ (1)	✓ (65)		✓ (14)
	Touch with genitals	Touch recipients' body with genital region	✓ (1)			
		Number of tactile gestures	8 (81)	13 (379)	9 (59)	13 (228)

Table S1. *Continued*

Visual	Arm raise	Lift arm(s) up in the air, approximately perpendicular to the ground	✓ (27)		✓ (25)	
	Extend arm	Hold out one's hand(s) or arm(s) to recipient	✓ (34)	✓ (15)	✓ (13)	✓ (10)
	Gallop	Run toward recipient in an exaggerated manner		✓ (2)		
	Hands around head	Lift arms up and place them around the head	✓ (2)		✓ (1)	
	Head shake	Move head or head and upper part of body rhythmically or only once (either vertical or horizontal; included nodding and bowing)	✓ (5)	✓ (101)	✓ (4)	✓ (7)
	Headstand	Turn vertically and stand on head and shoulders in front of recipient		✓ (1)		
	Ice skating	Perform a pirouette in front of recipient		✓ (6)	✓ (1)	
	Lay back	Lay down on the ground and raise limbs in the air	✓ (3)		✓ (7)	
	Move object	Move object (e.g., jute bag) on the ground	✓ (1)	✓ (2)		
	Offer	Present object, food or infant to recipient		✓ (5)		✓ (1)
	Offer body	Present a body part (e.g., back, head) to recipient		✓ (11)		✓ (13)
	Peer	Closely approach recipient and stare at its mouth or hands (while recipient is holding something of interest, e.g., food or performing a	✓ (48)	✓ (17)	✓ (33)	✓ (10)
	Present genitals	Present genital region to recipient by raising the abdomen towards recipient		✓ (8)		✓ (1)
	Shake	Shake limb(s) or whole body rhythmically; includes also kind of swinging around rope or bar	✓ (14)	✓ (4)	✓ (7)	✓ (1)
	Shake object	Wave object (e.g., rope) mainly with one's hand(s)	✓ (8)	✓ (5)	✓ (6)	✓ (4)
	Somersault	Turn a somersault on the ground		✓ (2)		
	Swagger	Move body rhythmically sidewise or back and forth while standing or sitting		✓ (5)		
	Throw object	Throw object towards recipient without hitting them		✓ (1)		
		Number of visual gestures	9 (142)	12 (177)	12 (105)	8 (47)

Table S1. *Continued*

Auditory						
	Beat object	Repeated, consecutive hits on ground, wall or object (see 'hit object' description) executed with the same body part (i.e., hand(s), arm(s) or foot/feet)	✓ (1)		✓ (3)	✓ (2)
	Body slap	Single hit of one's own body (except chest region) with hand(s)			✓ (1)	
	Foot stomp	Single and forceful step on the ground with one foot or both feet	✓ (13)	✓ (5)	✓ (9)	
	Hit object	Single and forceful hit on ground, wall, or object with hand(s) or arm(s)	✓ (6)		✓ (7)	
	Jump	Jump in a quadrupedal manner up and down in front of recipient	✓ (4)			
		Number of auditory gestures	4 (24)	1 (5)	4 (20)	1 (2)
		Total number	**21 (247)**	**26 (561)**	**25 (184)**	**22 (277)**

Behavioral context

	Access	Behavior related to the access of objects, such as offer access or prevent from access to an object	2 (3)	8 (18)	2 (5)	1 (2)
	Affiliation	Unaggressive approaches towards other individuals with the objective of decreasing distance and possibly establishing body contact), such as greeting events or requesting 'body closeness'	4 (28)	12 (141)	14 (41)	17 (120)
	Agonism	Aggressive behavior, possibly including physical contact, e.g., threatening or antagonistic encounters; also included less obvious aggressive behavior with the objective to increase distance between two individuals, such as displaying	4 (5)	13 (52)	2 (3)	6 (22)
	Grooming	Behavior accompanying grooming interactions, such as initiating or requesting grooming by offering ones own body	1 (3)	6 (17)		3 (9)
	Ingestion	Behavior concerning food intake, e.g., begging behavior; includes also nursing-related behavior	6 (58)	11 (95)	5 (29)	5 (17)
	Playing	Behavior to initiate or continue social play interactions, e.g., wrestling, chasing, or rough-and-tumble play, often accompanied by play face expression	19 (144)	17 (174)	18 (102)	8 (78)
	Sexual	Behavior accompanying mating interaction, e.g., presenting genitals		4 (12)		1 (1)
	Submission	Reassurance behavior after agonistic encounters, such as approaching a dominant individual		2 (3)		1 (3)
	Locomotion	Behavior accompanying the locomotion in the enclosure, e.g., initiating locomotion after a period of rest	2 (5)	6 (28)		6 (17)
	Unknown	Behavior that could not be classified	1 (1)	8 (21)	2 (4)	3 (8)

Table S2. Mean coefficient values for the three datasets of same zoo-housed and different zoo-housed dyads.

Species	Dyads compared	Dataset	Same zoo group		Different zoo group	
Bonobo	Infant-Infant	DICE C_D	0.53		0.65	
		At least once (Tau)	0.34	$N = 3$	0.19	$N = 12$
		Only both (Tau)	-0.12		0.15	
	Mother-Mother	DICE C_D	0.58		0.60	
		At least once (Tau)	0.08	$N = 3$	0.03	$N = 12$
		Only both (Tau)	0.02		0.25	
Chimpanzee	Infant-Infant	DICE C_D	0.50		0.54	
		At least once (Tau)	-0.04	$N = 1$	0.04	$N = 5$
		Only both (Tau)	-0.05		0.47	
	Mother-Mother	DICE C_D	0.62		0.57	
		At least once (Tau)	0.10	$N = 1$	0.01	$N = 5$
		Only both (Tau)	0.27		0.01	