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5   **Title: The Onset and Early Use of Gestural Communication in Nonhuman Great**

6   **Apes**

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8

9   **ABSTRACT**

10   The early gesturing of six bonobos, eight chimpanzees, three gorillas, and eight

11   orangutans was systematically documented using *focal animal sampling*. Apes' were

12   observed during their first 20 months of life in an effort to investigate; i) the onset of

13   gesturing; ii) the order in which signals of different sensory modalities appear; iii) the

14   extent to which infants make use of these modalities in their early signaling; and, iv) the

15   behavioral contexts where signals are employed. Orangutans differed in important

16   gestural characteristics to African ape species. Most notably, they showed the latest

17   gestural onset and were more likely to use their early signals in food-related

18   interactions. Tactile and visual signals appeared similarly early across all four species.

19   In African apes, however, visual signaling gained prominence over time, while tactile

20   signaling decreased. The current findings suggest that motor ability, which encourages

21   independence from caregivers, is an important antecedent, among others, in gestural

22   onset and development, a finding which warrants further investigation.

23
24   **Key words: gesture; onset; bonobo; chimpanzee; gorilla; orangutan**
25

26   **INTRODUCTION**

27   Gesturing is integral to human communication and plays a vital role in

28   children's early language, cognitive and social development [Bates et al., 1979; Capone

29   & McGregor, 2004; Crais, 2007; Goldin-Meadow, 1999; Gullberg et al., 2008; Kendon,

30   1988; McNeill, 1992; Tellier, 2009].   To further our understanding in this area of

31   nonvocal communication, researchers are turning their attention to the gestural behavior

32   of our closest living relatives, the nonhuman great apes [e.g., Call & Tomasello, 2007b;

33   Cartmill, 2008; Genty et al., 2009; Genty & Byrne, 2010; Liebal et al., 2006; Pika et al.,

34   2003, 2005b; Pollick, 2006; Tanner, 2004]. Doing so helps us to shed light on the roots

35   of human language and to identify traits that are shared or are unique to a species.

36   All four nonhuman great ape species (bonobo, chimpanzee, gorilla, and

37   orangutan) use gestures to communicate with their conspecifics. To qualify as a

38   gesture, the signal has to be directed towards a social partner, and the sender needs to

39   show anticipatory behavior of a response [Call & Tomasello, 2007b]. Through moving

40   limbs, head, or the whole body, apes demonstrate a pursuit of a goal with their

41   signaling, as well as an understanding of the signal's potential influence within a given

42   context [Call & Tomasello, 2007b]. A variety of gesture types in the tactile, visual, and

43   auditory sensory domains have been reported – although across all four species it is the

44   tactile and visual that are the more dominant [Tomasello et al., 1997; van Lawick-

45   Goodall, 1967]. Auditory gestures have been observed less in the African species and

46   not at all in orangutans [Liebal et al., 2006; Pika et al., 2005a]. The majority of gestures

47   initiate or announce a forthcoming action [Call & Tomasello, 2007b; cf., Schneider et

48   al., 2010] and are adapted to a number of different behavioral contexts, most notably

49   play in African species and food-related interactions in orangutans [Call & Tomasello,

50   2007a].

51   Most of what we know about the communicative abilities of our closest living

52   relatives derives from studies on subadult and adult individuals. Little attention has

53   been paid to the emergence and early characteristics of their signaling, and, hence, the

54   period of infancy is still poorly understood. Plooij [1978, 1984] has been the only

55   researcher to date to systematically study the onset and early use of gestural signaling.

56   Observing six feral mother-infant chimpanzee dyads with infants' ranging from 0 – 30

57   months, he found first gestures to appear around nine months of age. Only *ad hoc*

58   observations on the gestural onset exist in other ape species. Bard [1988, 1992]

59   observed free-ranging orangutans and their gesturing in food-sharing contexts within

60   mother-infant dyads. Five infants (aged one month to five years) were followed for

61   nine consecutive months. The author reported gestures from two years on – note,

62   however, there were no infants observed between 11 months and two years of age.

63   Liebal et al. [2006], while studying gestural communication in a predominant adult

64   group of captive orangutans, reported gesturing in an 11-month-old infant. Finally, Pika

65   et al. [2003, 2005b] observed a single bonobo, aged 13 months, and two gorillas, aged

66   16 and 20 months, employ gestures in their social interactions. The authors concluded

67   that the ability to communicate via gestures was fully developed in captive bonobos and

68   gorillas between one and two years of life. Collectively, these observations suggest that

69   gestural behavior emerges in all ape species between 1 – 1.5 years of age.

70   The onset of gestural communication is of particular interest with respect to the

71   varying life histories (i.e., the time-frame for important ontogenetic markers that

72   characterise a course of life) of nonhuman apes. Although all great apes share slow life

73   histories and long periods of dependent offspring when compared to other primates

74   [Read & Harvey, 1989; Kelley, 1997]; research suggests developmental rates still differ

75   among species. This is particularly true for orangutans and gorillas who straddle the

76   performance of bonobos and chimpanzees. Orangutans are thought to be the slowest

77   among all apes to reach their ontogenetic markers, e.g., gestation duration, weaning age,

78   interbirth interval [Wich et al., 2004, 2009] and gorillas the fastest, showing the shortest

79   infancy and juvenile stages [Bogin, 1999; Horwich, 1989; Watts & Pusey, 2002; Wich

80   et al., 2009].

81   To date no comparative study has been carried out on the early gestural

82   interactions in all four nonhuman great ape species. This is surprising given that for

83   several decades authors have considered such an approach to be essential to our overall

84   understanding of communication and its evolutionary roots [Cheney & Seyfarth, 1990;

85   Marler, 1976; Plooij, 1979]. The current study addressed this shortcoming. We

86   performed a longitudinal, observational study of bonobos, chimpanzees, gorillas, and

87   orangutans and systematically documented their gesturing during the first 20 months of

88   life. More specifically, our aim was to investigate; i) when infants start to gesture; ii)

89   the order in which signals of each sensory modality (tactile, visual, auditory) appear; iii)

90   the extent to which infants make use of these modalities in their early signaling; and, iv)

91   the behavioral contexts where signals are employed. Given the varying life histories in

92   the four species, we expected the ages of gestural onset to differ; with gorillas showing

93   the earliest and orangutans the latest onset across species. Onset differences were not

94   expected in the two genus *Pan* species. Finally, no predictions were made concerning

95   infants early use of signal modalities or the behavioral contexts where signals were

96   employed.

97   **METHODS**

98   The research adhered to the legal requirements of the countries in which it was

99   conducted, and to the principles of 'Ethical Treatment of Non-Human Primates', as

100   stated by the American Society of Primatologists.

101   **Subjects**

102   We observed six bonobos (*Pan paniscus*), eight chimpanzees (*Pan troglodytes*),

103   three gorillas (*Gorilla gorilla*), and eight orangutans (*Pongo pygmaeus*), ranging

104   between one and 20 months of age. They were born in captivity and lived in socially

105   housed groups in six European zoos. All infants, except one, were reared by their

106   biological mothers. The orangutan Dayang was raised by a foster mother from the

107   group. The zoo facilities and their arrangements varied, but all enclosures contained

108   climbing as well as resting opportunities, and several enrichment materials were

109   provided (e.g., wood wool). The daily routines of the apes were not disrupted by the

110   present research. Table I presents the sex, date of birth, species, and zoo affiliation of

111   each infant.

112   ------------
113   TABLE I
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115   **Observational procedure**

116   The first two authors and research assistants videotaped the observations

117   between July 2001 and August 2008. We observed each infant for four sessions per

118   month (four calendar weeks) using *focal animal sampling* [Altmann, 1974]. A session

119   lasted five minutes and was undertaken either once every week or twice every second

120   week. This resulted in 20 minutes of video footage per individual per month. The time

121   of observations varied throughout the day (between 8:30 a.m. and 7 p.m.), with sessions

122   for every subject distributed across the apes' diurnal activity. Infants were followed for

123   a minimum of four consecutive months and a maximum of 20, i.e., the total observation

124   time per infant ranged between 1.33 and 6.67 hours. On average, we observed each

125   species for 27 hours. Table II presents detailed information of the protocol for

126   observations and the analyses in which infants were included.

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128   TABLE II
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131   **Operational definitions and coding procedure**

132   Our operational definition of communication was adopted from Kimura [1993,

133   p. 3] and refers to "… the behaviors by which one member of a species conveys

134   information to another member of the species". We thereby focused on nonvocal

135   signals that served to achieve a social goal and aimed to change the immediate behavior

136   of the recipient. A gesture constituted the sender directing a motoric action (using head,

137   limb, or body movements) toward a recipient with anticipation of a reaction [adopted

138   from Call & Tomasello, 2007b; Wetherby et al., 1988]. The senders' action was

139   accompanied by orienting their body towards the recipient, gazing at them (before,

140   during or after signal) or by physical contact with them. The senders' anticipation of a

141   reaction was evidenced by gaze alignment, waiting, or persisting in the communicative

142   interaction [Bates et al., 1975; Bruner, 1981; Tomasello et al., 1994]. This definition

143   excludes simple mechanical actions produced to complete a desired outcome without

144   leaving the recipient the choice of action, e.g., to relocate another individual by

145   applying physical force [Call & Tomasello, 2007b]. Gestures were clustered into three

146   sensory categories [Tomasello et al., 1997]: tactile (signals were transferred by sharing

147   body contact with recipient, e.g., nudging), visual (signals were realised over distance

148   via particular body movements or postures, e.g., arm raising), and auditory (signals

149   were transmitted via an acoustic yet nonvocal sound, e.g., chest beating). If a gesture

150   incorporated more than one sensory mode, the tactile or auditory category was assigned

151   rather than visual, i.e., these gestures could be perceived even if the recipient was not

152   visually attending to them [Liebal, 2004].

153   For analysis, we played the footage through media player software and recorded

154   the coding in a spreadsheet application. The applied coding scheme was based upon

155   Tomasello et al. [1985] and Liebal et al. [2006], but was further adapted in respect to

156   the current research objectives.   For each gesture, we gathered the following

157   information: sex of sender, sex and age-class (infant: 0 – 2.5 years; juvenile: 2.6 – 5

158   years; subadult: 6 – 9 years; adult: ≥ 10 years) of recipient, gesture modality (tactile,

159   visual, and auditory), gesture type, and behavioral context as judged by the available

160   pre- and post information that accompanied the senders' signal. Table III presents

161   detailed descriptions of gesture types identified and the behavioral contexts in which

162   they were observed.

163   -------------
164   TABLE III
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166   **Interobserver reliability and analysis**

167   The first author coded all video footage. To ensure reliability, 20% of the data

168   were randomly chosen and coded by a naïve second person. We used Cohen's Kappa to

169   measure the degree of concordance between the two observers for gesture modality,

170   type, and behavioral context [Altman, 1991]. The resulting Kappa values 0.89 (for

171   modality), 0.84 (type), and 0.79 (context), according to Altman [1991] equate to a

172   "good" and "very good" level of agreement.

173   To analyze the order in which signal modalities appeared, we used a ranking

174   procedure. We assigned the ranks 1 – 3 to African apes (with "1" being the earliest and

175   "3" the latest), and ranks 1 and 2 to orangutans (since they displayed no auditory

176   signals). This also ensured that infants who had not displayed gestures in all possible

177   modalities were incorporated in the analysis. If an African infant only showed a single

178   sensory domain while being observed, we assigned the unseen modalities tied ranks.

179   For example, the gorilla Shaila (observed between 2 – 10 months) showed visual but no

180   tactile or auditory signals. We ranked her as follows: visual = 1, tactile and auditory =

181   2.5.

182   We used nonparametric tests for analyses. The Friedman and Wilcoxon tests

183   compared dependant samples, while the Kruskal-Wallis and Mann-Whitney U-tests

184   compared independent groups [Siegel & Castellan, 1988]. All P-values were two-tailed

185   and a null hypothesis was rejected at an alpha-level of 5%. As sample sizes were small,

186   we reported exact significances [Mundry & Fischer, 1998]. Moreover, we reported

187   effect sizes (using Pearson's correlation coefficient r) for the Wilcoxon and Mann-

188   Whitney U-tests [Field, 2005]. An effect size of .10 represents a small effect, .30 a

189   medium effect, and .50 a large effect [Cohen, 1988].

190   Sample sizes differed for particular analyses (see Table II); more detailed

191   information about these variations, and their rationale, is given in each respective results

192   subsection. The median was the chosen form of central tendency unless otherwise

193   stated.

194   **RESULTS**

195   **Overview of gestures**

196   We identified twenty-seven gesture types (10 tactile, 12 visual, and 5 auditory)

197   incorporating 298 gestures across all four ape species. No orangutan utilized any

198   auditory signal. Since the auditory mode has also not been observed in older orangutans

199   [Liebal et al., 2006; Pika et al., 2005a], we did not include this species in any analyses

200   considering this domain. One out of the eight orangutans, Maia, observed from two to

201   eight months, did not show any signals. Table IV presents the number of gesture types

202   observed (and their overall occurrences) per sensory modality and species.

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204   TABLE IV
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207   **Gestural onset**

208   To determine the gestural onset, we considered only subjects observed for at

209   least two consecutive months prior to their potential first gesture. This subsample

210   included 19 subjects (three bonobos, seven chimpanzees, three gorillas, six orangutans;

211   see Table II).

212   Fig. 1 presents the age of each infant when their first gesture appeared

213   (irrespective of sensory modality). We found differences between species (Kruskal-

214   Wallis test: $H(3) = 10.59$, $P = 0.004$; $N = 19$). *Post hoc* examinations yielded a

215   significant delayed onset in orangutans when compared with the three African ape

216   species (Mann-Whitney U-tests: gorilla, $U = 0$, $P = 0.012$, $r = -.80$; chimpanzee, $U = 4$,

217    $P = 0.012$, $r = -.69$; bonobo, $U = 0.5$, $P = 0.024$, $r = -.75$). The three African species

218   displayed, however, their first gesture at a similar age (bonobo versus chimpanzee: $U =$

219   6.5, $P = 0.467$, $r = -.30$; chimpanzee versus gorilla: $U = 9$, $P = 0.800$, $r = -.11$; bonobo

220   versus gorilla: $U = 0$, $P = 0.100$, $r = -.87$, note in this last comparison the small sample

221   sizes for both species and high effect size).

222   -------------
223   FIGURE 1
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225   **Emergence of tactile, visual and auditory gesturing**

226   Fig. 2 shows detailed information about the age at which gestures of each

227   sensory modality (tactile, visual, and auditory) were first observed in the 19 infants who

228   qualified for the onset analysis. By conducting the ranking procedure, we observed that

229   the ranks at which the tactile and visual modality appeared were similar in all species (N

230   = 19; tactile: $H(3) = 0.63$, $P = 0.921$; visual: $H(3) = 1.6$, $P = 0.676$). Auditory gestures

231   (considering only the African species) also emerged at similar positions in our ranking

232   system ($H(2) = 3.05$, $P = 0.266$; $N = 13$).

233   For African apes, some gesture modalities appeared earlier than others

234   (Friedman test: $\chi^2(2) = 14.94$, $P < 0.001$; $N = 13$). *Post hoc* testing revealed that

235   auditory signals were produced significantly later than both tactile (Wilcoxon test: $T =$

236   0, $P < 0.001$, $r = -.61$) and visual signals ($T = 3$, $P = 0.006$, $r = -.53$). The order that the

237   tactile and visual modalities appeared was similar ($T = 21$, $P = 0.339$, $r = -.22$). This

238   result was confirmed when orangutans were added to the analysis ($T = 53$, $P = 0.450$, r

239    $= -.13$; $N = 19$).

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241   FIGURE 2
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244   **Use of gestures over time**

245   *Sensory modality*

246   To explore the role of sensory modality in the production of gestures over time

247   (regardless of the respective signal types), we divided the observation period, of 9

248   months (the earliest median onset age for any species) to 20 months, into two time

249   periods; 9 − 14 months inclusive and 15 − 20 months inclusive. Here, we considered

250   only those individuals who were observed for at least one month in each time-block.

251   Since the three African species were similar in the order in which they first

252   displayed all three sensory modalities (tactile and visual together, auditory significantly

253   later), we compared them collectively over the two time-periods. Orangutans, who did

254   not start gesturing until a median age of 15 months, could only be considered in the

255   latter period 15 − 20 months. We contrasted their performances with those of African

256   apes in the earlier 9 − 14 months period. Overall these analyses incorporated six

257   orangutans and 15 African apes (six bonobos, seven chimpanzees, two gorillas; see

258   Table II).

259   Fig. 3 presents the mean percentages of signals used in each domain for African

260   apes and orangutans over the specified time periods. In African apes the proportion of

261   visual signals that were displayed increased significantly over the two periods ($T = 25$,

262    $P = 0.047$, $r = -.36$), while tactile gesturing significantly decreased ($T = 23$, $P = 0.035$, r

263    $= -.38$). For the auditory domain, we found a trend for an increase ($T = 3$, $P = 0.078$, $r =$

264    $-.34$).

265   Between 15 and 20 months of life, orangutans displayed a similar percentage of

266   tactile ($U = 38.5$, $P = 0.631$, $r = -.11$) and visual signals ($U = 42$, $P = 0.834$, $r = -.05$) to

267   that of African apes between 9 and 14 months (Fig. 3).

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270   FIGURE 3

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273   *Behavioral context*

274   We focused on the three main behavioral contexts in which infants employed

275   their gestures: play, ingestion, and affiliation. Single cases of additional contexts -

276   access, agonism, sexual, and locomotion - were assigned to the category "other".

277   As described above, African apes were compared across the two time periods,

278   while orangutans (15 – 20 months) were contrasted with the early performance of

279   African apes (9 – 14 months). Fig. 4 presents the mean percentages of signals

280   employed in the behavioral contexts observed for African apes and orangutans.

281   African apes did not reveal any significant context differences over time (play: *T*

282   = 29, *P* = 0.273, *r* = -.21; ingestion: *T* = 13, *P* = 0.160, *r* = -.27), although we found a

283   clear trend for a lower percentage of affiliation-related signals in slightly older apes (*T* =

284   11, *P* = 0.054, *r* = -.36). Within each time-block, however, more signals were

285   proportionally produced in certain contexts (9 – 14 months: $\chi^2(3) = 12.34$, *P* = 0.004; 15

286   – 20 months: $\chi^2(3) = 20.88$, *P* < 0.001). *Post hoc* testing revealed that infants produced

287   a significantly greater percentage of signals in the play context than in the ingestion (*T* =

288   5, *P* = 0.039, *r* = -.38) and than in "other" contexts (*T* = 0, *P* = 0.002, *r* = -.52) between

289   9 and 14 months. The proportion of play- and affiliation-related gestures that were

290   shown did not differ (*T* = 21.5, *P* = 0.318, *r* = -.19). Between 15 and 20 months of life,

291   signals were significantly more likely to be produced in play encounters than in any

292   other context (ingestion: *T* = 15, *P* = 0.016, *r* = -.43; affiliation: *T* = 3, *P* = 0.001, *r* = -

293   .57; "other": *T* = 5, *P* = 0.001, *r* = -.57).

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296   -------------

297   FIGURE 4

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300   Orangutans, in the 15 – 20 month period showed a greater percentage of food-

301   related signals than African apes in the 9 – 14 month period ($U = 16$, $P = 0.018$, $r = -$

302   .51).   No differences were detected for the play ($U = 42$, $P = 0.834$, $r = -.05$) and

303   affiliation context ($U = 40$, $P = 0.713$, $r = -.09$; Fig. 4).

304   **DISCUSSION**

305   In the present study we captured the onset of gestural communication in all four

306   nonhuman great ape species. Orangutans started gesturing at least four months later

307   than African apes, and, as previous research has also demonstrated [see Call &

308   Tomasello, 2007a], did not show any auditory gestures. While African apes made use

309   of all three signal modalities (tactile, visual, and auditory), auditory signals were only

310   employed after the onset of tactile and visual. In their first six months of gesturing, the

311   African species and orangutans displayed comparable proportions of tactile and visual

312   signals. African apes, however, showed an increase of visual signals at the expense of

313   tactile gestures with age. In terms of the behavioral contexts in which signals were

314   employed, orangutans showed proportionally more food-related signals than African

315   ape infants in their first six months of gesturing.

316   Regarding the gestural onset in chimpanzees, our data are largely consistent with

317   Plooij's [1978, 1984] systematic observation of wild conspecifics. Plooij observed the

318   first gestures around nine months, while in our sample the median age was 10 months

319   for chimpanzees. Compared with the African species, orangutans were the slowest to

320   start gesturing. This finding supports our prediction that Asian apes would differ in

321   their onset ages from other species as they are the slowest among all apes to reach their

322   ontogenetic markers (e.g., weaning age) [Wich et al., 2004, 2009]. Our data also

323   partially support the prediction that gorillas would be the fasted to gesture.   Gorillas

324   showed a possible accelerated onset when compared to bonobos, but not to chimpanzees

325   [see Pika et al., 2003 for similar observations in gorillas]. This coincides with our

326   knowledge of gorilla's expedited developmental trajectory [Bogin, 1999; Horwich,

327   1989; Watts & Pusey, 2002; Wich et al., 2009]. However, further research with larger

328   sample sizes is needed to further verify this conclusion.

329   We propose that infant's motility played an important part in the recognized

330   differences in gesturing development between the African ape species and orangutans.

331   Congruent with this premise was the fact that distal (i.e., visual) gesturing increased

332   over time at the expense of tactile signals in African apes. Tactile gestures appeared to

333   be more important to the infant when they were still bodily close to the mother or were

334   requesting 'comfort', but these were superseded by distal gestures as they matured and

335   gained independence. The trend for a proportional decline in affiliation-related signals

336   in these species (i.e., gestures that are used by infants to decrease distance from mother,

337   such as *extend arm*), also supports the idea of a motility-gestural onset link. Further

338   evidence of the importance of motility comes from our qualitative observations. Infants

339   with less-advanced locomotion (hence, higher rates of close-body contact with their

340   mother) displayed a slower gestural onset. Typically we observed this in orangutans

341   [see also Horwich, 1989; cf., Miller & Nadler, 1981]; but also elsewhere. For example,

342   one female chimpanzee (Kara) showed the latest gestural onset among her conspecifics

343   (15 months versus 10 months median onset age in chimpanzees) and was observed to be

344   the least independent from the mother.

345   As it has been hypothesized in human infants, the onset of locomotion has far-

346   reaching implications on the maturation of the perceptual system and cognitive

347   development in general [see Campos et al., 2000 for a review]. Moreover, it has been

348   proposed that the development of independent locomotion is intimately linked with the

349   emerging ability for social referencing within the mother-infant dyad [Bertenthal &

350   Campos, 1990; Rochat, 2004]. When starting to crawl, for example, infants use their

351   mother's emotional reaction as an information source in potentially dangerous situations

352   [Bertenthal & Campos, 1990].   Social referencing might, therefore, serve as the

353   connection between an infant's caregiver (who provides security) and the exploration of

354   the environment [Rochat, 2004].   We propose that further examining whether the

355   emergence of gestures is temporally associated with the onset of independent

356   locomotion, will enhance our knowledge of the processes involved in gestural

357   acquisition for human and other ape species.

358   In regard to the behavioral contexts in which signals were employed in their first

359   six months of gesturing, orangutans displayed a considerable higher proportion of

360   signals in food-related interactions than African apes. Similar contextual patterns have

361   been previously observed in older subjects [Call & Tomasello, 2007a]. An explanation

362   for this might be that African apes beg less for food as their mothers are more likely to

363   share. Recent studies seem to indicate that bonobos, for example, are more tolerant and

364   cooperative than other apes when it comes to food access and distribution [Hare et al.,

365   2007; Wobber et al., 2010; cf., Jaeggi et al., 2010].

366   Despite the different developmental trajectories of tactile and visual signals, both

367   emerged close in time and were shown in similar proportions in the first six months of

368   gesturing for all four species.   These findings emphasize the importance of visual

369   signaling in the apes' early life and thereby challenge the view that tactile signals are

370   dominant in youngsters – as previously proposed for chimpanzees [Tomasello &

371   Camioni, 1997]. Our data indicate a similar early manifestation of visual gestures (and

372   arguably underlying cognitive capacities) to that of human infants [see Crais, 2007]. In

373   regard to the visual domain, differing results have been reported in monkeys.

374   Grigor'eva and Deryagina [1987], who examined the early gestural communication in

375   stump-tailed macaques (*Macaca arctoides*) and hamadryas baboons (*Papio hamadryas*),

376   found that visual gestures appeared later than tactile gestures in their ontogeny, in fact,

377   in the early stages visual gestures were virtually nonexistent. Overall, therefore, signals

378   of the visual domain might have gained phylogenetic importance in human and

379   nonhuman great ape species but not in monkeys.

380   Although the present research is the largest explorative study on ape infants'

381   communication skills conducted to date, the data had various limitations. Most

382   importantly, sample sizes were small. Time constraints and other logistical obstacles

383   also meant that overall observation times for each species were limited, and individual

384   observation times varied (i.e., infants were observed for differing time periods during

385   their first 20 months). As a consequence, it was only possible to incorporate

386   subsamples in the analyses (e.g., only 19 of 25 subjects were included in onset-

387   analysis). Follow-up studies incorporating larger sample sizes and increased

388   observation times per individual could help strengthen the generalisability of our

389   findings.

390   In our exploration of apes' gestural beginnings, we found orangutans to differ

391   markedly from African apes. Most notably, and in accordance with their proposed slow

392   life history, orangutans were the slowest in gestural onset when compared with the

393   African species. However, there were also similarities. Comparable to humans, and

394   unlike monkeys, early gestures in all ape species were likely to be visual or tactile. This

395   may indicate the phylogenetic importance of the visual channel in early communication

396   in human and nonhuman ape species. It is suggested that motility is an important

397   ontogenetic antecedent embroiled in gestural acquisition and its development. The

398   extent that this may be the case is one of the intriguing questions this research has raised

399   and should be further explored.

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552 *TABLES*

TABLE I. Infant characteristics

Species	Infant	Sex	Date of Birth	Zoo
Bonobo	Habari	Male	29/01/06	Dierenpark Planckendael (B)
	Hongo	Male	25/02/06	Dierenpark Planckendael (B)
	Kivu	Male	24/02/07	Berlin Zoo (D)
	Huenda	Female	06/07/06	Dierenpark Planckendael (B)
	Luiza	Female	27/01/05	Leipzig Zoo (D)
	Nayembi	Female	26/04/06	Apenheul (NL)
Chimpanzee	Gihneau	Male	29/12/05	Burgers' Zoo (NL)
	Kofi	Male	07/07/05	Leipzig Zoo (D)
	Lobo	Male	21/04/04	Leipzig Zoo (D)
	Lome	Male	11/08/01	Leipzig Zoo (D)
	Kara	Female	23/06/05	Leipzig Zoo (D)
	Mora[†]	Female	23/06/07	Leipzig Zoo (D)
	Nafia	Female	10/06/06	Allwetterzoo Münster (D)
	Tai	Female	12/08/02	Leipzig Zoo (D)
Gorilla	Kibara	Female	13/01/04	Leipzig Zoo (D)
	Louna	Female	13/07/06	Leipzig Zoo (D)
	Shaila	Female	25/12/06	Burgers' Zoo (NL)
Orangutan	Güsa	Male	09/06/06	Burgers' Zoo (NL)
	Ito	Male	26/12/06	Allwetterzoo Münster (D)
	Pagai	Male	06/12/03	Leipzig Zoo (D)
	Dayang[‡]	Female	01/12/05	Apenheul (NL)
	Kila	Female	02/06/00	Leipzig Zoo (D)
	Maia	Female	07/12/07	Leipzig Zoo (D)
	Merah	Female	27/03/06	Apenheul (NL)
	Raja	Female	26/09/03	Leipzig Zoo (D)

[†]Infant died after suffering a bone fracture during observations; [‡]Infant was rejected by her mother soon after birth and was raised by a foster mother.

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TABLE II. Protocol for observations and analyses

Species	Infant	Frequency of observation	Observation period (initial-final age, in months)	Total observation time in hours	Analyses considered	
					General & modality onset	Modality & context use over time
Bonobo	Habari	Biweekly	13 – 20	2.7		✓
	Hongo	Biweekly	12 – 20	3		✓
	Kivu	Biweekly	2 – 20	6.3	✓	✓
	Huenda	Biweekly	7 – 16	3.3	✓	✓
	Luiza	Weekly	2 – 20	6.3	✓	✓
	Nayembi	Biweekly	12 – 19	2.2		✓
Chimpanzee	Gihneau	Biweekly	14 – 19	2		✓
	Kofi	Weekly	2 – 20	6.3	✓	✓
	Lobo	Weekly	1 – 20	6.7	✓	✓
	Lome	Weekly	2 – 20	6.3	✓	✓
	Kara	Weekly	2 – 20	6.3	✓	✓
	Mora	Weekly	1 – 11	3.7	✓	
	Nafia	Weekly	10 – 20	3.7	✓	✓
	Tai	Weekly	1 – 20	6.7	✓	✓
Gorilla	Kibara	Weekly	2 – 20	6.3	✓	✓
	Louna	Weekly	1 – 20	6.7	✓	✓
	Shaila	Biweekly	2 – 10	3	✓	
Orangutan	Güsa	Biweekly	8 – 13	2	✓	
	Ito	Weekly	3 – 20	6	✓	✓
	Pagai	Weekly	4 – 20	5.7	✓	✓
	Dayang	Biweekly	17 – 20	1.3		✓
	Kila	Weekly	16 – 19	1.3	✓	✓
	Maia	Weekly	2 – 8	2.3		
	Merah	Biweekly	13 – 20	2.7	✓	✓
	Raja	Weekly	6 – 19	4.7	✓	✓

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TABLE III. Gesture types identified and behavioral contexts distinguished across the four ape species

Coding category	Associated subcategories	Description
Gesture type & Modality		
Tactile	Arm on	Finger(s), hand(s), arm(s) were placed on any body part of the recipient; possibly holding on to recipients' body
	Body beat	Repeated, consecutive hits (see "hit" description) executed with the same body part (i.e., hand(s), arm(s), or foot (feet))
	Formal bite	Gentle bite of recipients' body (executed with mouth)
	Gentle touch	Very gentle touch or hold of recipients' body with finger(s), or hand(s)
	Hit	Single and forceful hit of recipients' body with hand(s), arm(s), or foot (feet)
	Lip-lip touch	Touch recipients' mouth with one's own mouth
	Nudge	Brief movement towards recipients' body with single finger(s), hand, or foot; also kind of pinch
	Push	Exert pressure on recipients' body with hand(s), arm(s), or foot (feet)
	Rest head	Place one's own head on recipients' body
	Touch with genitals	Touch recipients' body with genital region
Visual	Arm raise	Lift arm(s) up in the air, approximately perpendicular to the ground
	Extend arm	Hold out one's hand(s), or arm(s) to recipient
	Hands around head	Lift arms up and place them around the head
	Head shake	Move head or head and upper part of body rhythmically or only once (either vertical or horizontal; included *nodding* and *bowing*)
	Lay back	Lay down on the ground and raise limbs in the air
	Move object	Move object (e.g., jute bag) on the ground
	Peer	Closely approach recipient and stare at its mouth or hands (while recipient is holding something of interest, e.g., food, or performing a certain action)
	Running back	Move backwards
	Shake	Shake limb(s) or whole body rhythmically; includes also kind of swinging around rope or bar
	Shake object	Wave object (e.g., rope) mainly with one's hand(s)
	Somersault	Turn a somersault on the ground
	Swagger	Move body rhythmically sidewise or back and forth while standing or sitting
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))
	Body slap	Single hit of one's own body (except chest region) with hand(s)
	Chest beat	Repeated hits with alternating hand(s) on one's own chest
	Foot stomp	Single and forceful step on the ground with one foot or both feet
	Hit object	Single and forceful hit on ground, wall, or object with hand(s), or arm(s)
Behavioral context		
	Access	Behavior related to the access of objects, such as offer access or prevent from access to an object
	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'
	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
	Ingestion	Behavior concerning food intake, e.g., begging behavior; includes solid and fluid food
	Playing	Behavior to initiate or continue social play interactions, e.g., wrestling, chasing, or rough-and-tumble play, often accompanied by play face expression
	Sexual	Behavior accompanying mating interaction, e.g., presenting genitals
	Locomotion	Behavior accompanying the locomotion in the enclosure, e.g., initiating locomotion after a period of rest

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TABLE IV. Number of gesture types observed in the four ape species (in brackets: total number of occurrences)

Species	*Gesture types*			TOTAL
	tactile	visual	auditory	
Bonobo (*N* = 6)	4 (19)	9 (58)	2 (7)	15 (84)
Chimpanzee (*N* = 8)	5 (46)	10 (58)	2 (6)	17 (110)
Gorilla (*N* = 3)	3 (12)	5 (18)	4 (12)	12 (42)
Orangutan (*N* = 7*)	8 (35)	5 (27)	-	13 (62)

* One subject excluded.

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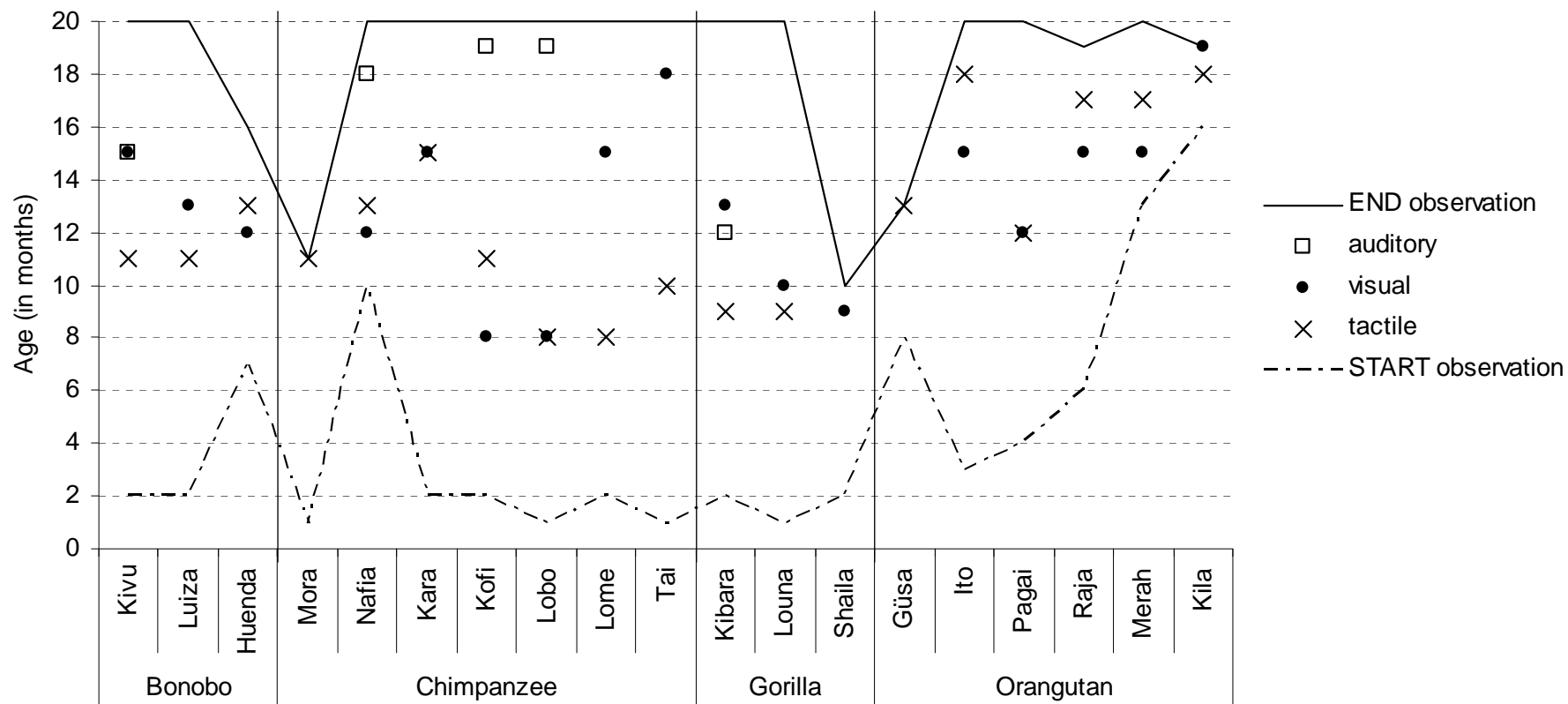
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577   *FIGURES*
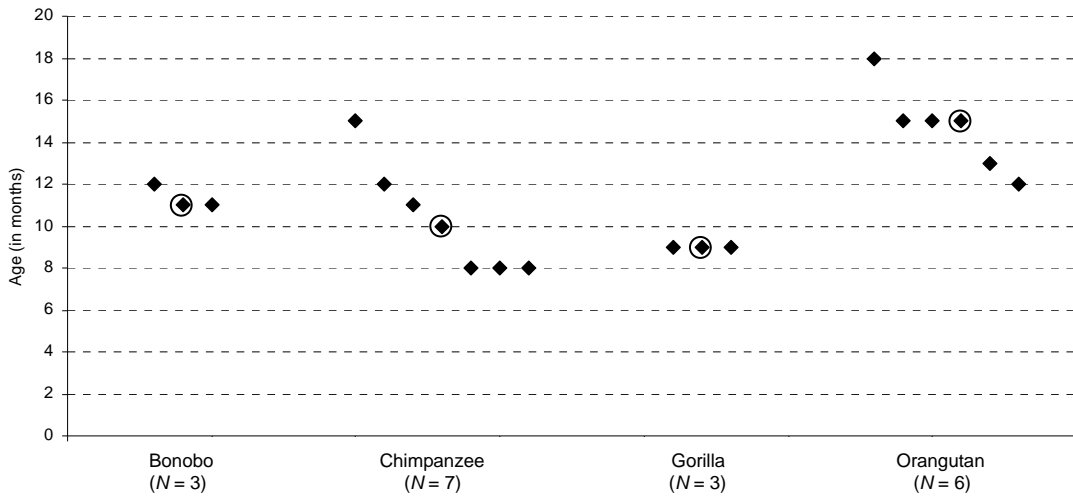
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580   **Fig. 1. Infants' gestural onset (*N* = 19; circle represents median onset age in each species).**
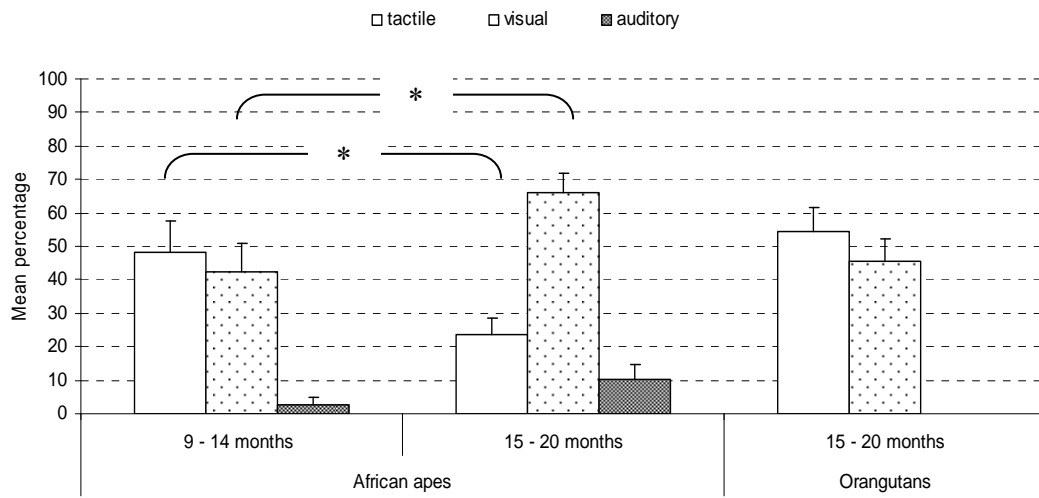
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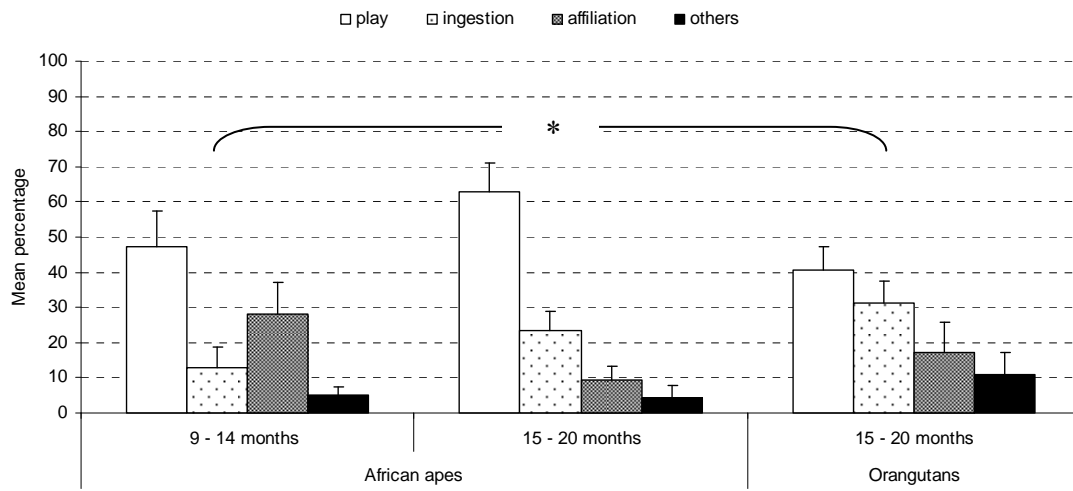584 **Fig. 2. First appearance of gestures in all four species broken down by the three sensory modalities ($N = 19$).**
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589 **Fig. 3. Mean percentages (plus standard error bar) for the three sensory modalities utilized by**
590 **African apes ($N = 15$) and orangutans ($N = 6$) in the specified time-periods (* $P < 0.05$).**
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594 **Fig. 4. Mean percentages (plus standard error bar) of the gesturing context for African apes (N =**
595 **15) and orangutans (N = 6) in the specified time-periods (* $P < 0.05$).**
596