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

ABSTRACT

The early gesturing of six bonobos, eight chimpanzees, three gorillas, and eight orangutans was systematically documented using *focal animal sampling*. Apes' were observed during their first 20 months of life in an effort to investigate; i) the onset of gesturing; ii) the order in which signals of different sensory modalities appear; iii) the extent to which infants make use of these modalities in their early signaling; and, iv) the behavioral contexts where signals are employed. Orangutans differed in important gestural characteristics to African ape species. Most notably, they showed the latest gestural onset and were more likely to use their early signals in food-related interactions. Tactile and visual signals appeared similarly early across all four species. In African apes, however, visual signaling gained prominence over time, while tactile signaling decreased. The current findings suggest that motor ability, which encourages independence from caregivers, is an important antecedent, among others, in gestural onset and development, a finding which warrants further investigation.

Key words: gesture; onset; bonobo; chimpanzee; gorilla; orangutan

INTRODUCTION

Gesturing is integral to human communication and plays a vital role in children's early language, cognitive and social development [Bates et al., 1979; Capone & McGregor, 2004; Crais, 2007; Goldin-Meadow, 1999; Gullberg et al., 2008; Kendon, 1988; McNeill, 1992; Tellier, 2009]. To further our understanding in this area of nonvocal communication, researchers are turning their attention to the gestural behavior of our closest living relatives, the nonhuman great apes [e.g., Call & Tomasello, 2007b; Cartmill, 2008; Genty et al., 2009; Genty & Byrne, 2010; Liebal et al., 2006; Pika et al., 2003, 2005b; Pollick, 2006; Tanner, 2004]. Doing so helps us to shed light on the roots of human language and to identify traits that are shared or are unique to a species.

All four nonhuman great ape species (bonobo, chimpanzee, gorilla, and orangutan) use gestures to communicate with their conspecifics. To qualify as a gesture, the signal has to be directed towards a social partner, and the sender needs to show anticipatory behavior of a response [Call & Tomasello, 2007b]. Through moving limbs, head, or the whole body, apes demonstrate a pursuit of a goal with their signaling, as well as an understanding of the signal's potential influence within a given context [Call & Tomasello, 2007b]. A variety of gesture types in the tactile, visual, and auditory sensory domains have been reported – although across all four species it is the tactile and visual that are the more dominant [Tomasello et al., 1997; van Lawick-Goodall, 1967]. Auditory gestures have been observed less in the African species and not at all in orangutans [Liebal et al., 2006; Pika et al., 2005a]. The majority of gestures initiate or announce a forthcoming action [Call & Tomasello, 2007b; cf., Schneider et al., 2010] and are adapted to a number of different behavioral contexts, most notably play in African species and food-related interactions in orangutans [Call & Tomasello, 2007a].

Most of what we know about the communicative abilities of our closest living relatives derives from studies on subadult and adult individuals. Little attention has been paid to the emergence and early characteristics of their signaling, and, hence, the period of infancy is still poorly understood. Plooij [1978, 1984] has been the only researcher to date to systematically study the onset and early use of gestural signaling. Observing six feral mother-infant chimpanzee dyads with infants' ranging from 0 – 30 months, he found first gestures to appear around nine months of age. Only *ad hoc* observations on the gestural onset exist in other ape species. Bard [1988, 1992] observed free-ranging orangutans and their gesturing in food-sharing contexts within mother-infant dyads. Five infants (aged one month to five years) were followed for nine consecutive months. The author reported gestures from two years on – note, however, there were no infants observed between 11 months and two years of age. Liebal et al. [2006], while studying gestural communication in a predominant adult group of captive orangutans, reported gesturing in an 11-month-old infant. Finally, Pika et al. [2003, 2005b] observed a single bonobo, aged 13 months, and two gorillas, aged 16 and 20 months, employ gestures in their social interactions. The authors concluded that the ability to communicate via gestures was fully developed in captive bonobos and gorillas between one and two years of life. Collectively, these observations suggest that gestural behavior emerges in all ape species between 1 – 1.5 years of age.

The onset of gestural communication is of particular interest with respect to the varying life histories (i.e., the time-frame for important ontogenetic markers that characterise a course of life) of nonhuman apes. Although all great apes share slow life histories and long periods of dependent offspring when compared to other primates [Read & Harvey, 1989; Kelley, 1997]; research suggests developmental rates still differ among species. This is particularly true for orangutans and gorillas who straddle the performance of bonobos and chimpanzees. Orangutans are thought to be the slowest among all apes to reach their ontogenetic markers, e.g., gestation duration, weaning age, interbirth interval [Wich et al., 2004, 2009] and gorillas the fastest, showing the shortest infancy and juvenile stages [Bogin, 1999; Horwich, 1989; Watts & Pusey, 2002; Wich et al., 2009].

To date no comparative study has been carried out on the early gestural interactions in all four nonhuman great ape species. This is surprising given that for several decades authors have considered such an approach to be essential to our overall understanding of communication and its evolutionary roots [Cheney & Seyfarth, 1990; Marler, 1976; Plooij, 1979]. The current study addressed this shortcoming. We performed a longitudinal, observational study of bonobos, chimpanzees, gorillas, and orangutans and systematically documented their gesturing during the first 20 months of life. More specifically, our aim was to investigate; i) when infants start to gesture; ii) the order in which signals of each sensory modality (tactile, visual, auditory) appear; iii) the extent to which infants make use of these modalities in their early signaling; and, iv) the behavioral contexts where signals are employed. Given the varying life histories in the four species, we expected the ages of gestural onset to differ; with gorillas showing the earliest and orangutans the latest onset across species. Onset differences were not expected in the two genus *Pan* species. Finally, no predictions were made concerning infants early use of signal modalities or the behavioral contexts where signals were employed.

METHODS

The research adhered to the legal requirements of the countries in which it was conducted, and to the principles of 'Ethical Treatment of Non-Human Primates', as stated by the American Society of Primatologists.

Subjects

We observed six bonobos (*Pan paniscus*), eight chimpanzees (*Pan troglodytes*), three gorillas (*Gorilla gorilla*), and eight orangutans (*Pongo pygmaeus*), ranging between one and 20 months of age. They were born in captivity and lived in socially housed groups in six European zoos. All infants, except one, were reared by their biological mothers. The orangutan Dayang was raised by a foster mother from the group. The zoo facilities and their arrangements varied, but all enclosures contained climbing as well as resting opportunities, and several enrichment materials were provided (e.g., wood wool). The daily routines of the apes were not disrupted by the present research. Table I presents the sex, date of birth, species, and zoo affiliation of each infant.

TABLE I

Observational procedure

The first two authors and research assistants videotaped the observations between July 2001 and August 2008. We observed each infant for four sessions per month (four calendar weeks) using *focal animal sampling* [Altmann, 1974]. A session lasted five minutes and was undertaken either once every week or twice every second week. This resulted in 20 minutes of video footage per individual per month. The time of observations varied throughout the day (between 8:30 a.m. and 7 p.m.), with sessions for every subject distributed across the apes' diurnal activity. Infants were followed for a minimum of four consecutive months and a maximum of 20, i.e., the total observation time per infant ranged between 1.33 and 6.67 hours. On average, we observed each species for 27 hours. Table II presents detailed information of the protocol for observations and the analyses in which infants were included.

TABLE II

Operational definitions and coding procedure

Our operational definition of communication was adopted from Kimura [1993, p. 3] and refers to "… the behaviors by which one member of a species conveys information to another member of the species". We thereby focused on nonvocal signals that served to achieve a social goal and aimed to change the immediate behavior of the recipient. A gesture constituted the sender directing a motoric action (using head, limb, or body movements) toward a recipient with anticipation of a reaction [adopted from Call & Tomasello, 2007b; Wetherby et al., 1988]. The senders' action was accompanied by orienting their body towards the recipient, gazing at them (before, during or after signal) or by physical contact with them. The senders' anticipation of a reaction was evidenced by gaze alignment, waiting, or persisting in the communicative interaction [Bates et al., 1975; Bruner, 1981; Tomasello et al., 1994]. This definition excludes simple mechanical actions produced to complete a desired outcome without leaving the recipient the choice of action, e.g., to relocate another individual by applying physical force [Call & Tomasello, 2007b]. Gestures were clustered into three sensory categories [Tomasello et al., 1997]: tactile (signals were transferred by sharing body contact with recipient, e.g., nudging), visual (signals were realised over distance via particular body movements or postures, e.g., arm raising), and auditory (signals were transmitted via an acoustic yet nonvocal sound, e.g., chest beating). If a gesture incorporated more than one sensory mode, the tactile or auditory category was assigned rather than visual, i.e., these gestures could be perceived even if the recipient was not visually attending to them [Liebal, 2004].

For analysis, we played the footage through media player software and recorded the coding in a spreadsheet application. The applied coding scheme was based upon Tomasello et al. [1985] and Liebal et al. [2006], but was further adapted in respect to the current research objectives. For each gesture, we gathered the following information: sex of sender, sex and age-class (infant: 0 – 2.5 years; juvenile: 2.6 – 5 years; subadult: 6 – 9 years; adult: ≥ 10 years) of recipient, gesture modality (tactile, visual, and auditory), gesture type, and behavioral context as judged by the available pre- and post information that accompanied the senders' signal. Table III presents detailed descriptions of gesture types identified and the behavioral contexts in which they were observed.

TABLE III

Interobserver reliability and analysis

The first author coded all video footage. To ensure reliability, 20% of the data were randomly chosen and coded by a naïve second person. We used Cohen's Kappa to measure the degree of concordance between the two observers for gesture modality, type, and behavioral context [Altman, 1991]. The resulting Kappa values 0.89 (for modality), 0.84 (type), and 0.79 (context), according to Altman [1991] equate to a "good" and "very good" level of agreement.

To analyze the order in which signal modalities appeared, we used a ranking procedure. We assigned the ranks 1 – 3 to African apes (with "1" being the earliest and "3" the latest), and ranks 1 and 2 to orangutans (since they displayed no auditory signals). This also ensured that infants who had not displayed gestures in all possible modalities were incorporated in the analysis. If an African infant only showed a single sensory domain while being observed, we assigned the unseen modalities tied ranks. For example, the gorilla Shaila (observed between 2 – 10 months) showed visual but no tactile or auditory signals. We ranked her as follows: visual = 1, tactile and auditory = 2.5.

We used nonparametric tests for analyses. The Friedman and Wilcoxon tests compared dependant samples, while the Kruskal-Wallis and Mann-Whitney U-tests compared independent groups [Siegel & Castellan, 1988]. All *P*-values were two-tailed and a null hypothesis was rejected at an alpha-level of 5%. As sample sizes were small, we reported exact significances [Mundry & Fischer, 1998]. Moreover, we reported effect sizes (using Pearson's correlation coefficient *r*) for the Wilcoxon and Mann-Whitney U-tests [Field, 2005]. An effect size of .10 represents a small effect, .30 a medium effect, and .50 a large effect [Cohen, 1988].

Sample sizes differed for particular analyses (see Table II); more detailed information about these variations, and their rationale, is given in each respective results subsection. The median was the chosen form of central tendency unless otherwise stated.

RESULTS

Overview of gestures

We identified twenty-seven gesture types (10 tactile, 12 visual, and 5 auditory) incorporating 298 gestures across all four ape species. No orangutan utilized any auditory signal. Since the auditory mode has also not been observed in older orangutans [Liebal et al., 2006; Pika et al., 2005a], we did not include this species in any analyses considering this domain. One out of the eight orangutans, Maia, observed from two to eight months, did not show any signals. Table IV presents the number of gesture types observed (and their overall occurrences) per sensory modality and species.

TABLE IV

Gestural onset

To determine the gestural onset, we considered only subjects observed for at least two consecutive months prior to their potential first gesture. This subsample included 19 subjects (three bonobos, seven chimpanzees, three gorillas, six orangutans; see Table II).

Fig. 1 presents the age of each infant when their first gesture appeared (irrespective of sensory modality). We found differences between species (Kruskal-Wallis test: $H(3) = 10.59$, $P = 0.004$; $N = 19$). *Post hoc* examinations yielded a significant delayed onset in orangutans when compared with the three African ape species (Mann-Whitney U-tests: gorilla, $U = 0$, $P = 0.012$, $r = -.80$; chimpanzee, $U = 4$, $P = 0.012$, $r = -.69$; bonobo, $U = 0.5$, $P = 0.024$, $r = -.75$). The three African species displayed, however, their first gesture at a similar age (bonobo versus chimpanzee: $U = 6.5$, $P = 0.467$, $r = -.30$; chimpanzee versus gorilla: $U = 9$, $P = 0.800$, $r = -.11$; bonobo versus gorilla: $U = 0$, $P = 0.100$, $r = -.87$, note in this last comparison the small sample sizes for both species and high effect size).

FIGURE 1

Emergence of tactile, visual and auditory gesturing

Fig. 2 shows detailed information about the age at which gestures of each sensory modality (tactile, visual, and auditory) were first observed in the 19 infants who qualified for the onset analysis. By conducting the ranking procedure, we observed that the ranks at which the tactile and visual modality appeared were similar in all species ($N = 19$; tactile: $H(3) = 0.63$, $P = 0.921$; visual: $H(3) = 1.6$, $P = 0.676$). Auditory gestures (considering only the African species) also emerged at similar positions in our ranking system ($H(2) = 3.05$, $P = 0.266$; $N = 13$).

For African apes, some gesture modalities appeared earlier than others (Friedman test: $\chi^2(2) = 14.94$, $P < 0.001$; $N = 13$). *Post hoc* testing revealed that auditory signals were produced significantly later than both tactile (Wilcoxon test: $T = 0$, $P < 0.001$, $r = -.61$) and visual signals ($T = 3$, $P = 0.006$, $r = -.53$). The order that the tactile and visual modalities appeared was similar ($T = 21$, $P = 0.339$, $r = -.22$). This result was confirmed when orangutans were added to the analysis ($T = 53$, $P = 0.450$, $r = -.13$; $N = 19$).

FIGURE 2

Use of gestures over time

Sensory modality

To explore the role of sensory modality in the production of gestures over time (regardless of the respective signal types), we divided the observation period, of 9 months (the earliest median onset age for any species) to 20 months, into two time periods; 9 – 14 months inclusive and 15 – 20 months inclusive. Here, we considered only those individuals who were observed for at least one month in each time-block.

Since the three African species were similar in the order in which they first displayed all three sensory modalities (tactile and visual together, auditory significantly later), we compared them collectively over the two time-periods. Orangutans, who did not start gesturing until a median age of 15 months, could only be considered in the latter period 15 – 20 months. We contrasted their performances with those of African apes in the earlier 9 – 14 months period. Overall these analyses incorporated six orangutans and 15 African apes (six bonobos, seven chimpanzees, two gorillas; see Table II).

Fig. 3 presents the mean percentages of signals used in each domain for African apes and orangutans over the specified time periods. In African apes the proportion of visual signals that were displayed increased significantly over the two periods ($T = 25$, $P = 0.047$, $r = -.36$), while tactile gesturing significantly decreased ($T = 23$, $P = 0.035$, $r = -.38$). For the auditory domain, we found a trend for an increase ($T = 3$, $P = 0.078$, $r = -.34$).

Between 15 and 20 months of life, orangutans displayed a similar percentage of tactile ($U = 38.5$, $P = 0.631$, $r = -.11$) and visual signals ($U = 42$, $P = 0.834$, $r = -.05$) to that of African apes between 9 and 14 months (Fig. 3).

FIGURE 3

Behavioral context

We focused on the three main behavioral contexts in which infants employed their gestures: play, ingestion, and affiliation. Single cases of additional contexts - access, agonism, sexual, and locomotion - were assigned to the category “other”.

As described above, African apes were compared across the two time periods, while orangutans (15 – 20 months) were contrasted with the early performance of African apes (9 – 14 months). Fig. 4 presents the mean percentages of signals employed in the behavioral contexts observed for African apes and orangutans.

African apes did not reveal any significant context differences over time (play: $T = 29$, $P = 0.273$, $r = -.21$; ingestion: $T = 13$, $P = 0.160$, $r = -.27$), although we found a clear trend for a lower percentage of affiliation-related signals in slightly older apes ($T = 11$, $P = 0.054$, $r = -.36$). Within each time-block, however, more signals were proportionally produced in certain contexts (9 – 14 months: $\chi^2(3) = 12.34$, $P = 0.004$; 15 – 20 months: $\chi^2(3) = 20.88$, $P < 0.001$). *Post hoc* testing revealed that infants produced a significantly greater percentage of signals in the play context than in the ingestion ($T = 5$, $P = 0.039$, $r = -.38$) and than in “other” contexts ($T = 0$, $P = 0.002$, $r = -.52$) between 9 and 14 months. The proportion of play- and affiliation-related gestures that were shown did not differ ($T = 21.5$, $P = 0.318$, $r = -.19$). Between 15 and 20 months of life, signals were significantly more likely to be produced in play encounters than in any other context (ingestion: $T = 15$, $P = 0.016$, $r = -.43$; affiliation: $T = 3$, $P = 0.001$, $r = -.57$; “other”: $T = 5$, $P = 0.001$, $r = -.57$).

FIGURE 4

Orangutans, in the 15 – 20 month period showed a greater percentage of food-related signals than African apes in the 9 – 14 month period ($U = 16$, $P = 0.018$, $r = -.51$). No differences were detected for the play ($U = 42$, $P = 0.834$, $r = -.05$) and affiliation context ($U = 40$, $P = 0.713$, $r = -.09$; Fig. 4).

DISCUSSION

In the present study we captured the onset of gestural communication in all four nonhuman great ape species. Orangutans started gesturing at least four months later than African apes, and, as previous research has also demonstrated [see Call & Tomasello, 2007a], did not show any auditory gestures. While African apes made use of all three signal modalities (tactile, visual, and auditory), auditory signals were only employed after the onset of tactile and visual. In their first six months of gesturing, the African species and orangutans displayed comparable proportions of tactile and visual signals. African apes, however, showed an increase of visual signals at the expense of tactile gestures with age. In terms of the behavioral contexts in which signals were employed, orangutans showed proportionally more food-related signals than African ape infants in their first six months of gesturing.

Regarding the gestural onset in chimpanzees, our data are largely consistent with Plooij's [1978, 1984] systematic observation of wild conspecifics. Plooij observed the first gestures around nine months, while in our sample the median age was 10 months for chimpanzees. Compared with the African species, orangutans were the slowest to start gesturing. This finding supports our prediction that Asian apes would differ in their onset ages from other species as they are the slowest among all apes to reach their ontogenetic markers (e.g., weaning age) [Wich et al., 2004, 2009]. Our data also partially support the prediction that gorillas would be the fasted to gesture. Gorillas showed a possible accelerated onset when compared to bonobos, but not to chimpanzees [see Pika et al., 2003 for similar observations in gorillas]. This coincides with our knowledge of gorilla's expedited developmental trajectory [Bogin, 1999; Horwich, 1989; Watts & Pusey, 2002; Wich et al., 2009]. However, further research with larger sample sizes is needed to further verify this conclusion.

We propose that infant's motility played an important part in the recognized differences in gesturing development between the African ape species and orangutans. Congruent with this premise was the fact that distal (i.e., visual) gesturing increased over time at the expense of tactile signals in African apes. Tactile gestures appeared to be more important to the infant when they were still bodily close to the mother or were requesting 'comfort', but these were superseded by distal gestures as they matured and gained independence. The trend for a proportional decline in affiliation-related signals in these species (i.e., gestures that are used by infants to decrease distance from mother, such as *extend arm*), also supports the idea of a motility-gestural onset link. Further evidence of the importance of motility comes from our qualitative observations. Infants with less-advanced locomotion (hence, higher rates of close-body contact with their mother) displayed a slower gestural onset. Typically we observed this in orangutans [see also Horwich, 1989; cf., Miller & Nadler, 1981]; but also elsewhere. For example, one female chimpanzee (Kara) showed the latest gestural onset among her conspecifics (15 months versus 10 months median onset age in chimpanzees) and was observed to be the least independent from the mother.

As it has been hypothesized in human infants, the onset of locomotion has far-reaching implications on the maturation of the perceptual system and cognitive development in general [see Campos et al., 2000 for a review]. Moreover, it has been proposed that the development of independent locomotion is intimately linked with the emerging ability for social referencing within the mother-infant dyad [Bertenthal & Campos, 1990; Rochat, 2004]. When starting to crawl, for example, infants use their mother's emotional reaction as an information source in potentially dangerous situations [Bertenthal & Campos, 1990]. Social referencing might, therefore, serve as the connection between an infant's caregiver (who provides security) and the exploration of the environment [Rochat, 2004]. We propose that further examining whether the emergence of gestures is temporally associated with the onset of independent locomotion, will enhance our knowledge of the processes involved in gestural acquisition for human and other ape species.

In regard to the behavioral contexts in which signals were employed in their first six months of gesturing, orangutans displayed a considerable higher proportion of signals in food-related interactions than African apes. Similar contextual patterns have been previously observed in older subjects [Call & Tomasello, 2007a]. An explanation for this might be that African apes beg less for food as their mothers are more likely to share. Recent studies seem to indicate that bonobos, for example, are more tolerant and cooperative than other apes when it comes to food access and distribution [Hare et al., 2007; Wobber et al., 2010; cf., Jaeggi et al., 2010].

Despite the different developmental trajectories of tactile and visual signals, both emerged close in time and were shown in similar proportions in the first six months of gesturing for all four species. These findings emphasize the importance of visual signaling in the apes' early life and thereby challenge the view that tactile signals are dominant in youngsters – as previously proposed for chimpanzees [Tomasello & Camioni, 1997]. Our data indicate a similar early manifestation of visual gestures (and arguably underlying cognitive capacities) to that of human infants [see Crais, 2007]. In regard to the visual domain, differing results have been reported in monkeys. Grigor'eva and Deryagina [1987], who examined the early gestural communication in stump-tailed macaques (*Macaca arctoides*) and hamadryas baboons (*Papio hamadryas*), found that visual gestures appeared later than tactile gestures in their ontogeny, in fact, in the early stages visual gestures were virtually nonexistent. Overall, therefore, signals of the visual domain might have gained phylogenetic importance in human and nonhuman great ape species but not in monkeys.

Although the present research is the largest explorative study on ape infants' communication skills conducted to date, the data had various limitations. Most importantly, sample sizes were small. Time constraints and other logistical obstacles also meant that overall observation times for each species were limited, and individual observation times varied (i.e., infants were observed for differing time periods during their first 20 months). As a consequence, it was only possible to incorporate subsamples in the analyses (e.g., only 19 of 25 subjects were included in onset-analysis). Follow-up studies incorporating larger sample sizes and increased observation times per individual could help strengthen the generalisability of our findings.

In our exploration of apes' gestural beginnings, we found orangutans to differ markedly from African apes. Most notably, and in accordance with their proposed slow life history, orangutans were the slowest in gestural onset when compared with the African species. However, there were also similarities. Comparable to humans, and unlike monkeys, early gestures in all ape species were likely to be visual or tactile. This may indicate the phylogenetic importance of the visual channel in early communication in human and nonhuman ape species. It is suggested that motility is an important ontogenetic antecedent embroiled in gestural acquisition and its development. The extent that this may be the case is one of the intriguing questions this research has raised and should be further explored.

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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.

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	✓	✓

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

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.

FIGURES

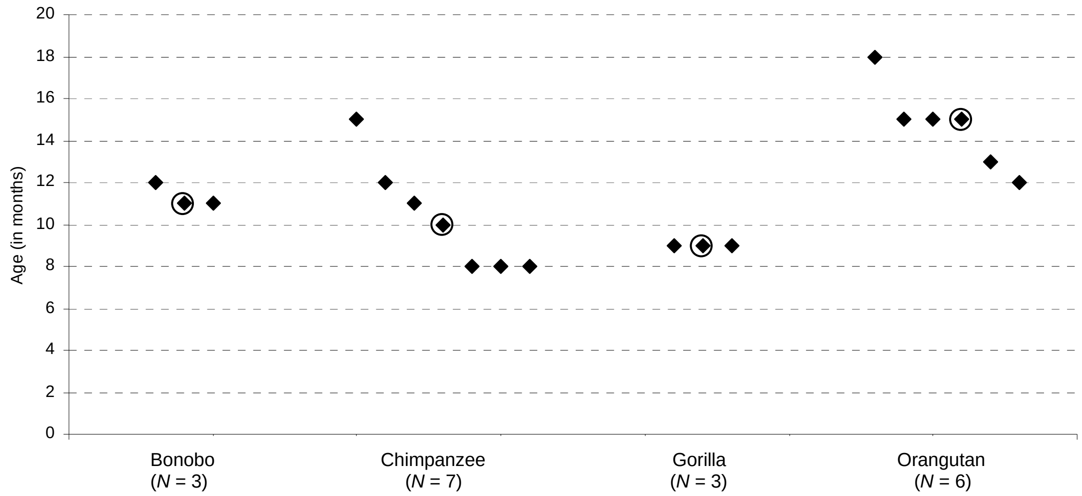

Fig. 1. Infants' gestural onset (*N* = 19; circle represents median onset age in each species).

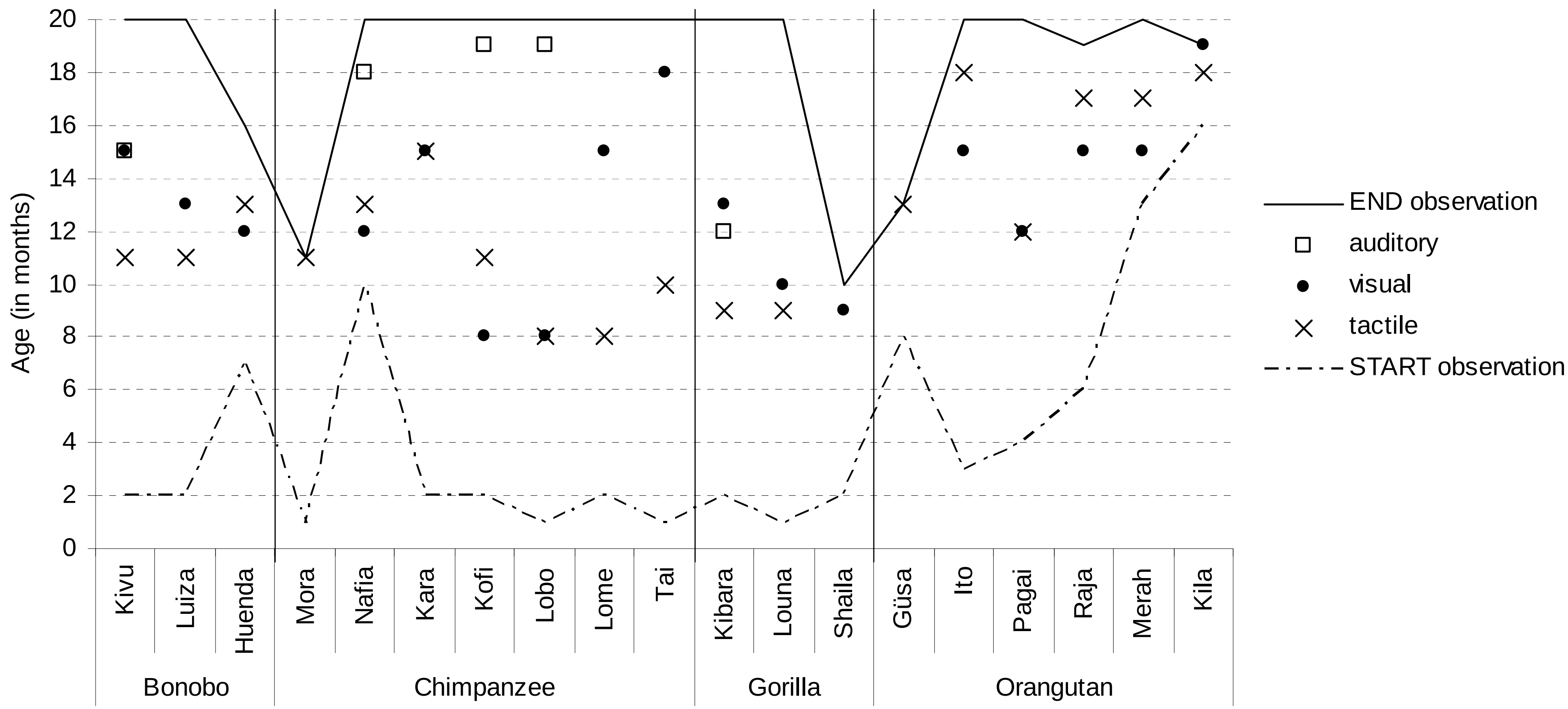

Fig. 2. First appearance of gestures in all four species broken down by the three sensory modalities (*N* = 19).

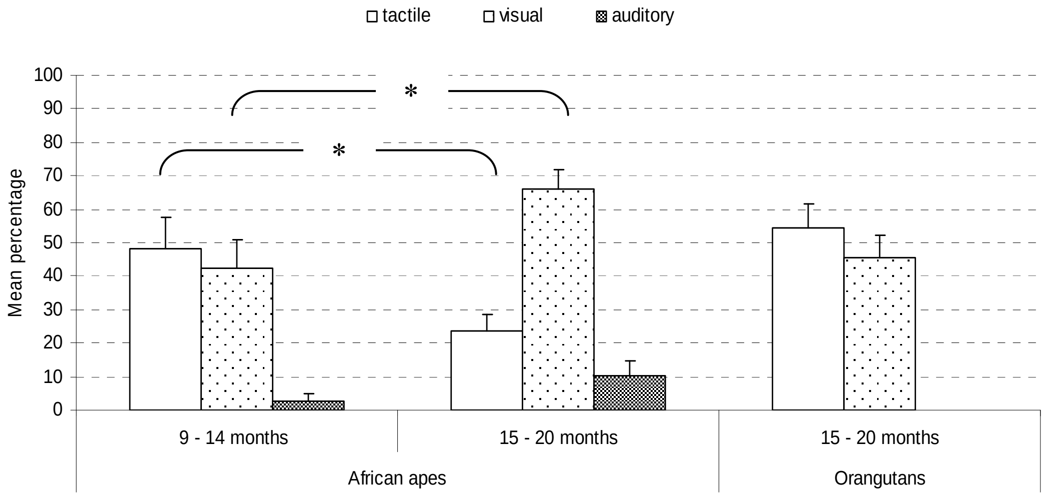

Fig. 3. Mean percentages (plus standard error bar) for the three sensory modalities utilized by African apes ($N = 15$) and orangutans ($N = 6$) in the specified time-periods (* $P < 0.05$).

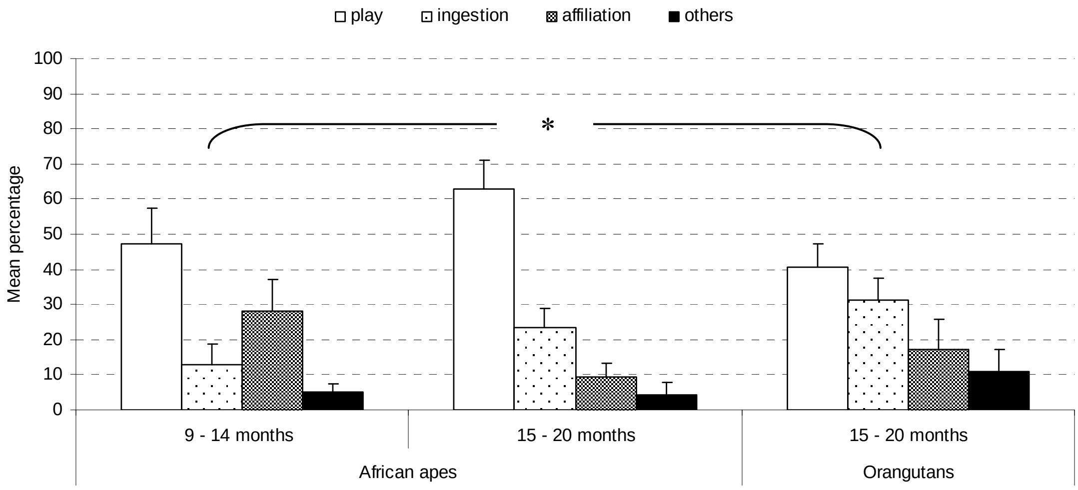

Fig. 4. Mean percentages (plus standard error bar) of the gesturing context for African apes (*N* = 15) and orangutans (*N* = 6) in the specified time-periods (* *P* < 0.05).