

Gestural communication of orangutans (*Pongo pygmaeus*)

Katja Liebal¹, Simone Pika², and Michael Tomasello³

¹Portsmouth University, UK / ²University of St. Andrews, Scotland, UK /

³Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany

This study represents a systematic investigation of the communicative repertoire of Sumatran orangutans (*Pongo pygmaeus abelii*), with a focus on intentional signals in two groups of captive orangutans. The goal was to analyze the signal repertoire with respect to (1) the number and frequency of signals (gestures, facial expressions, and actions), (2) the variability of individual repertoires as a function of group, age class, and sex, and (3) the flexibility of use in terms of ‘means-end dissociation’ and ‘audience effects’ and to interpret the findings in terms of the ecology, social structure and socio-cognitive skills of orangutans. The results show that orangutans use a remarkable number of signals including tactile and visual gestures as well as several more complex actions, though few facial expressions and no auditory gestures were observed. One third of signals were used within a play context, followed by one fourth of interactions in the context of ingestion. Although the repertoire included several visual gestures, most of the signals produced were tactile gestures and they were used particularly in the contexts of affiliation and agonism, whereas visual gestures dominated in the context of grooming, ingestion and sexual behavior. Individual repertoires showed a remarkable degree of variability as a function of age and group affiliation. Orangutans used their signals flexibly in several functional contexts and adjusted the signal they used depending on the attentional state of the recipient, similar to findings of other great ape species and gibbons. Thus, the communicative behavior of orangutans is characterized by a variable and flexible use of signals possibly reflecting their highly variable social structure and their sophisticated socio-cognitive skills, with the dominance of tactile gestures corresponding to the arboreal nature of this species.

Keywords: *Pongo pygmaeus*, communication, gestures, facial expressions, flexibility

Introduction

The majority of research on nonhuman primate communication has been concerned with vocal communication (Seyfarth, 1987; Crockford, Herbinger, Vigilant, & Boesch, 2004; Hohmann & Fruth, 1995), which seems to have derived from the analogy to human language and an approach within the framework of a vocal origin of spoken language (MacNeilage, 1987; Snowdon, 2001; Aiello, 1998; Marler, 1998). However, recent research has shown that human language does not rely only on the spoken modality with gestures also being important as communicative means (Kendon, 2004; Goldin-Meadow, 2002, Iverson, 2001). In addition, non-vocal communicative systems have been shown to develop similar properties as spoken language (Senghas, Kita, & Özyürek, 2004). Hence, there is an increasing interest in the study of non-vocal communicative behavior of nonhuman primates within the framework of a gestural origin of human language (Hewes, 1973; Corballis, 2002; King, 1999, 2004).

Several studies of different monkey and ape species show that gestures play an important role in communication between conspecifics, and that they are used flexibly in a number of different functional contexts to achieve particular social goals. For example, the gestures used by pigtail macaques (*Macaca nemestrina*) vary as a function of context, such as dominance/ submission, sexual context or affiliative behavior (Maestripietri, 1996). Similar results were found for both small and great apes in a series of comparative studies including siamangs (Liebal, Pika, & Tomasello, 2004), gorillas (Pika, Liebal, & Tomasello, 2003), chimpanzees (Tomasello, George, Kruger, Farrar, & Evans, 1985; Tomasello, Gust, & Frost, 1989; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994; Tomasello, Call, Warren, Frost, Carpenter, & Nagell, 1997) and bonobos (Pika, Liebal, & Tomasello, 2005). All these species use a variety of gestures and facial expressions within several functional contexts and adjust the signals they use depending on the behavior of the individual they interact with. However, species differences have been found in both the type and number of signals used, reflecting different ecological conditions, social structures and cognitive skills (Pika, 2002).

In contrast to the African great ape species, the gestural communication of orangutans along with their socio-cognitive abilities has not been well investigated. As opposed to the other great apes, orangutans are characterized by an almost exclusively arboreal lifestyle in the tropical rain forest of restricted areas in Sumatra and Borneo (Rijksen & Meijaard, 1999).

Previously, orangutans were considered a solitary species, but this view has changed with more information about the social organization of this species

(Rijksen & Meijaard, 1999). Overall, there are three basic social units that include (a) adult females with their offspring, (b) adolescent and/ or subadult individuals of both sexes, and (c) solitary, adult males (MacKinnon, 1974; Rodman, 1973; Rijksen, 1978; Horr, 1975). A minority of adults live as residents within their ranges, but most individuals are nomadic and are present in a certain area for several weeks or months, and a few wanderers being only seen in a certain area infrequently or once. However, this status of an individual is variable and changes during ontogeny (Rijksen & Meijaard, 1999). Since ranges of several individuals can overlap, different social units can aggregate to form temporary associations or social groups during feeding in the same fruit tree or traveling (MacKinnon, 1974; Rijksen, 1978; Rijksen & Meijaard, 1999; Galdikas & Vasey, 1992). However, adult males are particularly intolerant of other adult males and except during periods of sexual consortships they are truly solitary, spending less than 2% of their time with other individuals (Galdikas, 1985).

Thus, the social structure of orangutans is characterized by a high degree of variation in individual social behavior depending on sex, age, reproductive state and social status. The semi-solitary social organization of orangutans can therefore be described as an individual-based fission-fusion system highly variable over space and time (van Schaik, 1999).

In terms of their cognitive skills, captive orangutans, at least, have been observed to deploy a number of sophisticated skills in both the physical and social cognitive domain. They use and manufacture tools (Lethmate, 1977, 1982) and even outperform chimpanzees in certain tasks such as the manipulation of objects (Parker, 1969). Galdikas and Vasey (1992) describe how wild orangutans recognize other members of their species as individuals and know the personal relationships they share with them. Although Kaplan and Rogers (2002) found that orangutans avoid gazing directly at conspecifics, they do follow the gaze direction of a human experimenter at a ceiling or around barriers, suggesting that they do not just orient to a shared target but actually attempt to take the visual perspective of another individual (Bräuer, Call, & Tomasello, 2005).

However, since sophisticated socio-cognitive skills are usually correlated with the social complexity of primate groups (Whiten & Byrne, 1997), the extraordinary intelligence of orangutans seems to be paradoxical in regard to their semi-solitary lifestyle (Delgado & van Schaik, 2000). Therefore, it is important to study their communicative system and the strategies they use to deal with the great amount of variability of their social relationships. Some authors have found that orangutans use a wide range of vocal signals and gestures (Kaplan & Rogers, 2000; MacKinnon, 1974) while others speculate that they

might have lesser communication skills because of their semi-solitary lifestyle (Bennett, 1998). In addition, their natural habitat seems to predict the importance of tactile or vocal signals over visual signals since an individual's view is restricted by dense vegetation (Marler, 1965; Maestripiერი, 1999). However, most studies are restricted to an overall description of some gestures and facial expressions within the general behavioral repertoire of orangutans (Rijksen, 1978; Maple, 1980; MacKinnon, 1974; Jantschke, 1972). There are no systematic investigations of the individual variability of the communicative repertoire and the flexibility of use in different functional contexts. With the exception of Bard (1992) who describes the ontogeny of intentional communication in young orangutans in the context of food-sharing, there are no studies concerning the communicative behavior of orangutans and the cognitive aspects of their communication.

The focus of this paper is on intentional social communication of captive Sumatran orangutans (*Pongo pygmaeus abelii*) by means of different signal categories (gestures, facial expressions, and actions) with regard to individual variability and flexibility. The variability may be pronounced in differences between individual repertoires as a function of group, age or sex; flexibility can be considered in two ways: (1) So-called 'means-end dissociation' is the use of a particular signal in different functional contexts and/or diverse signals for one functional context. Therefore the signaling individual uses different means to reach a particular social goal. Those communicative strategies can be varied depending on previous interactions with the recipient (Tomasello et al., 1997). (2) The 'audience effect' is defined as the sender's sensitivity to the presence/absence of a potential recipient as well as the choice of signals depending on the attentional state of the recipient. To prompt a recipient's reaction, tactile gestures and most of the actions can be performed either towards an attending or not attending recipient, whereas visual gestures and facial expressions can only cause a reaction if the recipient is already attending.

The aims of this study were (1) to document all intentional signals used by different individuals in two captive groups of Sumatran orangutans including adults and their offspring of different age classes and to document the functional context of each signal; (2) to establish individual differences in signals used with respect to group, age, and sex; and (3) to provide some account of the cognitive processes involved, focusing on the flexible use and signal sequences in terms of adaptability for specific communicative circumstances.

According to Maestripiერი (1999), the gestural repertoire of orangutans living in a egalitarian-individualistic society that lacks a strong dominance hierarchy and strong bonds between group members (with the exception

of mothers and their offspring) should be characterized by a high degree of variability because of a selective pressure to develop complex patterns of affiliative communication and bonding between unrelated individuals. However, because of their semi-solitary nature, interactions should take place mainly between dyads of mothers and their offspring, and interactions between group members should be less frequent in comparison to primates living in more social groups. And so for ecological, social, and cognitive reasons, it was expected that orangutans use a highly variable repertoire of gestures, facial expressions and actions, with tactile gestures being more frequent than visual gestures given their arboreal lifestyle.

Methods

Subjects

A total of 16 individuals was observed in two captive groups. The observations were conducted by one observer (first author) in May through July 2001 on the group at Leipzig Zoo, Germany, and in February through March 2002 on the group at Zuerich Zoo, Switzerland. Table 1 shows the individuals and their main characteristics such as their group affiliation, name, sex, age at the beginning of the observation period and the corresponding age class. The classification of age classes was largely adopted from Rijksen (1978), but here it was not distinguished between subadult and adult males according to the developmental status (unflanged versus flanged); all males older than 10 years were considered as adult males. The group at Leipzig Zoo consisted of seven individuals ranging from 11 months through 28 years. There were two adult males (>10), two adult females (>10 years), one subadult female (5–10), one juvenile (2½–5) and one infantile female (0–2½). The group at Zuerich Zoo consisted of nine individuals ranging from 4.5 through approximately 41 years. The group consisted of two adult males, four adult females, two subadult females and one juvenile female. All together, there were ten adult orangutans, three subadults, two juveniles and one infantile individual representing four males and twelve females. All individuals except one (*Pongo*) were born in captivity.

The Leipzig group was housed at the Wolfgang Köhler Primate Research Center in an indoor and outdoor enclosure containing several trees, ropes and platforms. The observations were conducted in both the indoor and outdoor enclosure from both special observation platforms above the orangutan enclosure and from the visitor area, where the apes were separated by ditches

Table 1. Individuals observed in the present study: Names, sex, age at the beginning of the observation period and the corresponding age class are shown in association with group affiliation.

Group	Name	Sex	Age (years/months)	Age class
Leipzig	Dunja	Female	28.1	Adult
	Bimbo	Male	21.8	Adult
	Pini	Female	12.11	Adult
	Walter	Male	12.1	Adult
	Toba	Female	7.3	Subadult
	Padana	Female	3.6	Juvenile
	Kila	Female	0.11	Infantile
	Zuerich	Pongo	Male	ca. 41
Lea		Female	34.6	Adult
Timor		Female	26.9	Adult
Selatan		Female	18.9	Adult
Oceh		Female	13.11	Adult
Djaro		Male	11.8	Adult
Salih		Female	9.2	Subadult
Tuah		Female	8.6	Subadult
Xira		Female	4.5	Juvenile

or glass windows from the humans. According to the daily routine, the orangutans had the possibility to retreat into their sleeping cages where they were not visible for the observer.

The Zuerich group was housed in one large and a small indoor cage that contained several trees, robes and sleeping nests. The observations were conducted from the visitor area through glass plates separating the apes from the visitors.

Both groups were fed several times a day with a diet consisting of a balanced and varying mixture of vegetables, fruits and greens supplemented by pellets, seeds and insects. No changes in their daily routine except of the presence of the observer were required for the conduct of this study.

Procedure

According to the methods used in Liebal et al. (2004), focal-animal-sampling (Altmann, 1974) was used to observe each of the 16 individuals for a total of 10 hours. A digital video camera (SONY DCR-TRV900E) was used to record the orangutans' behavior resulting in a total of 160 hours on tape. This method

enabled calculation of the total frequencies of particular signals and therefore allowed comparisons across individuals, groups, age classes and sex. Every focal animal was selected in a random order and was videotaped in 15-minute bouts. If a subject moved outside the range of vision, the recording was stopped, and if it did not return within five minutes, the next session with a new focal animal was started. Daily observations took place between 8.30 am and 6 pm with the observation bouts equally distributed over the daily activity period of the apes.

The videotapes were analyzed on a digital video recorder (SONY MiniDV) with a slow-playback-function. All signals sent by the focal animal or directed towards it were transferred into a spreadsheet-coding scheme. Furthermore, all signals that did not include the focal animal as sender or recipient, but another interacting pair of individuals present on the videotape, were also recorded. Signals that occurred during an ongoing interaction (e.g. within a play sequence) were not coded. That means the focus was on signals that aimed to initiate a response of the recipient. However, if a signal appeared after an interruption of an interaction for at least five seconds it was included in the further analysis.

Intentional communication was defined as a motoric act directed to a recipient via body orientation, eye gaze or physical contact with the sender expecting a response as evidenced by looking to the recipient, waiting for a response or persisting in the communicative interaction (Sarimski, 2002; Tomasello et al., 1985, 1994). Applying the following three criteria, an observed behavior was thus defined as an intentional signal if it (1) was observed at least two times over the whole observation period (which ensured that this gesture served to reach a recurrent social goal); (2) was directed at a particular recipient; and (3) was used flexibly in different social contexts, or else several signals were all used in the same context ['means-end dissociation' (Bruner, 1981)]. Therefore, 'intentional communication' in this study implied that the sender considered the recipient as a social agent and adjusted its communicative means by augmentation, addition or substitution of the signal until the social goal was obtained (Bard, 1992; Bates, 1979). Inflexible expressions of the subject's emotional state — that is, those not accompanied by response-waiting, persistence, or means-ends dissociation — were not recorded.

To label the observed signals, new terms were established to provide an objective description of the communicative behavior instead of applying already existing definitions from other studies. The signals were classified into three signal categories:

1. Gestures: expressive movements of limbs or head and body postures. Tactile gestures, including physical contact between the interacting animals, were distinguished from visual gestures, which were distant signals and represented movements of different body parts or specific body postures.
2. Facial expressions: expressive movements of different parts of the face, such as the mouth, lips and eyes, were classified as a special kind of visual signal.
3. Actions: as opposed to gestures, actions did not represent a particular, delimited expressive movement or body posture, but rather a complex series of movements for which it was not possible to determine which particular component of this series was initiating a recipient's response.

For every recorded signal the following was coded:

1. Focal animal, sender, recipient
2. Attentional state of the recipient: 'Attending' was defined as the recipient having direct eye contact with the signaling individual or his body being oriented towards the sender and having him in his field of vision. In contrast, 'not attending' was when the recipient's head was turned away from the sender or if his attention was not directed towards the sender but distracted by other social partners or incidents in his environment.
3. Response of the recipient (within a time interval of five seconds): (a) No reaction of the recipient, (b) a change of the recipient's state of attention from 'not attending' to 'attending' without a further reaction to the preceded signal, or (c) the signal causes a reaction of the recipient which can be classified into a particular functional context such as play or aggression.
4. Functional context: access (to objects or doors to get access to adjacent cages), affiliation, agonism, ingestion, parental care, play, social grooming, sexual behavior, submissive behavior, and walk. Signals that could not be connected with a particular context were labeled as unknown.
5. Combinations: a signal could be performed (1) as single signal or (2) simultaneously together with another signal at the same time or (3) as part of a successive combination (= sequence) which was defined as one sender performing two or more signals towards the same recipient in the same context and within five seconds of one another. In the present paper, only the results for successive combinations are shown.

Statistics

To assess reliability, the observer (first author) coded all videotapes and 20% of the data were coded by a second person (second author). Cohen's Kappa was used to measure their agreement in the definition of signals which was a 0.77 corresponding to a 'good' level of agreement (Altman, 1991).

Non-parametric tests were used for data analysis. All tests were two-tailed and a null-hypothesis was rejected at an alpha-level of 5%. Exact tests were used when the sample size was smaller than 10 per group. If not described differently, median (\bar{x}) numbers or proportions of individual performance are presented. For the analysis of signal sequences only pooled data could be used, since some of the individuals only rarely combined signals. For sender-recipient interactions, the results are presented as mean proportions of interactions per dyad based on the total of interactions within a group.

With regard to the distribution of signals within and between the two groups, the degree of concordance of the individual signal repertoires was analyzed within each group as well between groups according to the method described in Bakeman and Gottman (1997). Cohen's kappa was used to measure within-group agreement in signal performance by calculating the median kappa for each dyad of individuals based on the total number of signals each individual performed and how many of them were also present in the other individual's repertoire of the compared dyad. Finally, these median kappas were divided by the number of dyads within this group. Analogously, between-group kappas were calculated out of all median kappas between each individual of one group and each individual of the other group and divided by the number of all dyads between the two groups. A Wilcoxon-test was applied to compare each individual's median kappa within each group to members of the other group.

Spearman's correlations were used to analyze the degree of relationship between two different variables. Friedman-tests were applied to compare more than two dependent variables followed by Wilcoxon-tests for pairwise comparison in case the Friedman-test found significant differences. In case of independent variables, the analogous procedure was applied using a Kruskal-Wallis test first followed by Mann-Whitney U-tests to analyze two independent variables. To control for multiple comparisons, all *p*-values of pairwise comparisons were adjusted by using Bonferroni-Hochberg correction (Shaffer, 1995).

Results

Signal repertoire and frequency

A total of 2112 signals were observed and a repertoire containing 44 distinct signals was established including 14 tactile gestures, 15 visual gestures, five facial expressions and 10 actions. No auditory gestures were produced. Table 2 shows these signals together with a short description according to their signal modality and their total frequency. Overall, frequently used tactile gestures were ‘pull’ (258), ‘slap’ (170) or ‘push’ (144); ‘approach face’ (149) was the most frequent visual gesture (Table 2). ‘Wrestle’ (211) was the most often used action and ‘open mouth’ (85) the most frequent observed facial expression. Other signals, such as ‘headstand’, ‘hold hand in front of the mouth’ and ‘jerking body movements’ were each observed only twice. Some of the gestures, such as ‘shake object’, ‘throw object’ and ‘present object’ were object based and involved the use of ropes, branches or other objects. Occasionally, individuals used branches or sticks to ‘slap’ or ‘nudge’ another orangutan.

Considering signal categories, individuals used tactile gestures most often (\bar{x} = 47.9%) followed by actions (\bar{x} = 20.1%), visual gestures (\bar{x} = 19.1%) and facial expressions (\bar{x} = 4.6%). Tactile gestures were performed significantly more often than all other signal categories. Facial expressions were used least often (Friedman-test: $\chi^2 = 35.06$, $df = 3$, $p < 0.001$; Wilcoxon-test: tactile gestures versus visual gestures: $Z = -3.103$, $p = 0.004$, $N = 16$; tactile gestures versus facial expression: $Z = -3.561$, $p < 0.001$, $N = 16$; tactile gestures versus actions: $Z = -2.741$, $p < 0.001$, $N = 16$; facial expressions versus visual gestures: $Z = -2.613$, $p < 0.001$, $N = 15$; facial expressions versus actions: $Z = -2.327$, $p = 0.004$, $N = 15$; visual gestures versus actions: $Z = -2.964$, $p = 0.63$, $N = 15$).

Comparison with other studies

Table 3 summarizes a number of studies on captive and wild orangutans in comparison with the signals of the current study and the major functional contexts in which the signals were used. Rijksen (1978) mentions a number of “gestures and postures involving a clear taxis component with reference to a social partner” in both wild and rehabilitant Sumatran orangutans. With regard to tactile gestures, MacKinnon (1974) found a *kiss* gesture between young orangutans and mothers possibly resembling the ‘lip touch’ gesture of the present study also mentioned by Rijksen (1978, *mouth–mouth contact*). Rijksen (1978) observed it mostly in the context of ingestion, but also within playful

Table 2. Signals observed according to their signal category in association with a short description and the total frequency of each signal.

Tactile gestures	Description	Frequency
Bite in hand	Sender gentle bites the recipient in its hand	15
Embrace	Sender approaches recipient frontally or laterally and puts one or two of his arms around the body of the recipient	6
Formal bite	Sender touches the recipient with its open mouth on any body part and bites it with a low intensity	97
Gentle touch	Sender touches the social partner gently with hand or foot on any body part	123
Hold tight	Sender seizes the hand or foot of the recipient	26
Lip touch	Sender approaches with its face the face of the recipient, touching its mouth with its lips; can be accompanied by embracing the recipient's head with one arm	94
Nudge	Sender touches the recipient with single fingers, knuckles or fist (as opposed to 'slap' which is performed by using the flat hand or rear palm of the hand)	49
Pull	Sender grasps any body part of the recipient by hand or foot and then performs a short, forceful movement with it	258
Push	Sender pushes any body part of the recipient with a short, vigorous movement away	144
Put face on face	Sender approaches the face of the recipient, taking the others mouth into its slightly open mouth	3
Put hand on head	Sender puts its flat hand on the head or back of the recipient and remains there	5
Slap	Sender hits the recipient with a flat hand at any body part	170
Throw object	Sender throws an object at another individual	5
Touch with genital region	Sender hangs in front of the recipient and touches its face with its genital region (is an intensification of the visual gesture 'present genitals')	7

interactions. Wild orangutans perform gestures such as touch, poking, hitting or grabbing (MacKinnon, 1974; Rijksen, 1978) which were also observed in captivity (Jantschke, 1972; Becker, 1984; Maple, 1980). The 'formal bite' of the present study is mentioned by Rijksen (1978) as *mock bite*.

The visual gesture 'wave arm' has also been observed by other studies in captivity (Jantschke, 1972) as well as in the wild (MacKinnon, 1974; Rijksen, 1978, *arm waving*). 'Bite intention' of the present study is equivalent to *lunge* observed by MacKinnon (1974) whereas Rijksen (1978) recorded *muzzle pushing* which consisted of bite intention movements combined with tactile components such as pushing another individual's hand, food or head away with its

Table 2. (continued)

Visual gestures		
Approach face	Sender approaches the face of another individual staring at the others mouth; sometimes eye contact is established	149
Bite intention	Sender indicates a rapid movement with its upper part of its body and the 'open mouth' towards the recipient, but stops in this forward movement without physical contact	38
Extend arm	Sender extends its arm towards the recipient; the palm of the hand is not directed upwards	30
Hand shake	Sender shakes its hands around the wrist	9
Headstand	Sender turns vertically and stands on its head and shoulders	2
Hit intention	Sender performs a movement with its arm as if to hit and remains without physical contact with the recipient	12
Hold hand in front of the mouth	Sender puts its extended arm with the palm directed upwards in front of the mouth of another individual	2
Jerking body movements	Sender hangs in front of the recipient and moves the body up and down by angling its arms repeatedly.	2
Offer arm with food pieces	Sender chews leaves or fruits into its fur of the arm and then extends its arm to present the food to another individual	15
Offer body part	Sender offers any body part for grooming	33
Offer food	Sender extends its arm with a piece of food in its hand and holds it in front of the mouth of the recipient.	24
Present genitals	Sender sits or hangs in front of the recipient and raises its posterior to present its genital region	28
Present object	Sender presents an object by extending the arm with the object in its hands or by hiding under an object	11
Shake object	Sender shakes an object	30
Wave arm	Sender extends its arm and waves it horizontally in front of its own body	4

muzzle. This seems more like the tactile gesture 'put face to face' of the present study. Jantschke (1972) observed similar *hit- and bite intentions* during aggressive encounters of captive orangutans. *Look at mouth* (Rijksen, 1978) corresponds to the 'approach the face' gesture of the present study. According to Rijksen (1978), this gesture is used in the food context and is always performed by the younger or lower ranking individual. *Presenting* (here: 'present genitals') is usually described in a sexual context in wild orangutans, but it has also been shown to function as a reassurance gesture after aggressive encounters (Rijksen, 1978). Rijksen (1978) mentions *self-decorate*, which might be a similar behavior to the gesture 'present object' of the present study. The 'extend arm'

Table 2. (continued)

Facial expressions		
Grin	Sender opens its mouth slightly with the corners of the mouth pulled back and the teeth scarcely visible between the lips; teeth can be either closed or slightly opened	13
Pout face	Sender protrudes its lips forming a round 'trumpet'-like shape	6
Protruded lips	Sender protrudes its lips similar to 'pout face', but upends its upper lip; the teeth are visible	14
Open mouth	Sender has its mouth open to the full extent with the canine teeth and the palate visible; the lips form an elliptical shape (corners not retreated)	85
Relaxed open mouth actions	Sender has its mouth opened, teeth are not closed, the corners of the mouth are slightly withdrawn	7
Bite	Sender bites the recipient on any body part; as opposed to the 'formal bite' this is not only a hinted signal but is performed with higher intensity	130
Box	Sender hits the other with both fists quickly and repeatedly in its upper part of the body	28
Chase	Sender approaches the recipient running, climbing or brachiating	39
Jump at	Sender jumps at the recipient or drops on him out of a hanging position	59
Rock	Sender moves the upper part of its body to and fro while sitting	12
Swing	Sender hangs in front of the recipient and rocks its body to and fro with rapid movements	58
Swing headfirst	As before, but sender initiates the interaction while hanging headfirst	12
Wrestle	Sender approaches the recipient and starts to tussle with him. This action can be accompanied by biting or slapping	211
Wrestle head-first	As before, but sender initiates the interaction while hanging headfirst	43
Walk backwards	Sender slowly walks backwards ('bluff chase'); may pause and start again repeatedly	4

gesture has also been described for wild orangutans (Rijksen, 1978; *hold out hand*) and captive individuals (Maple, 1980, *hand extension*). In the present study it was observed in the play context or in mother-offspring interactions, but Rijksen (1978) also refers to its function as a reassurance gesture directed from a lower-ranking individual toward the dominant one. In the current study, the 'hold hand in front of the mouth' gesture with the palm of the open

Table 3. Signals used by orangutans of the current study in comparison to other publications of captive and wild orangutans, respectively. For each signal the corresponding reference and its functional contexts in which it was observed are shown. Signals are ordered alphabetically within their corresponding signal category.

Signal	Liebal, Pika and Tomasello		Other captive studies		Studies in the wild	
	Functional context	Signal [Translation] (reference)	Functional context	Signal	Functional context	Signal
Tactile gestures						
Bite in hand	affiliation, play	Biting hands/feet (Maple, 1980)	play			
Embrace	affiliation, parental care			Embrace (MacKinnon, 1974, Rijksen, 1978)	affiliation, parental care	
Formal bite	access, agonistic, play, sexual			Mock bite (Rijksen, 1978)	play	
Gentle touch		<i>Anfassen</i> [touch] (Becker, 1984)	play	Touch (Rijksen, 1978)	contact/affiliation	
Lip touch	ingestion, play, affiliation			Kiss (?) (MacKinnon, 1974)	food, play	
Pull	all contexts except submissive	<i>Ziehen</i> [pull] (Becker, 1984, Jantschke, 1972)	play	Mouth-mouth contact (Rijksen, 1978)	play	
Push	all contexts except submissive	Hair pulling (Zucker et al., 1978)	play	Grasp (Rijksen, 1978)	play	
Put face to face	affiliation, play	Push/dragging (Zucker et al., 1978)	play			
Slap	agonism, ingestion, play, sexual	Head butting (Maple, 1980)	play	Muzzle-pushing (?) (Rijksen, 1978)	play, food	
		<i>Schlagen</i> [hit] (Becker, 1984)	play	Hitting (Rijksen, 1978)		
		Slapping (Maple, 1980)	play			
		Face-stroking (Zucker et al., 1978)	play			
Throw object	affiliation, play	<i>Objekt werfen</i> [throw object] (Becker, 1984)	play	Throwing (Rijksen, 1978)	play	

Table 3. (continued)

Visual gestures					
Approach the face		affiliation, grooming, ingestion		Look at mouth (Rijksen, 1978)	ingestion/food
Bite intention	agonistic, grooming, play		<i>Beijfintention</i> [bite intention] (Jantschke, 1972)	Lunge (MacKinnon, 1974)	intimidation/agonism
Extend arm	affiliation, ingestion, play		Handextension (Maple, 1980)	Hold out hand (Rijksen, 1978)	parental care, affiliation, submission
Hit intention	agonistic, play		<i>Handausstrecken</i> [handextension] (Becker, 1984)		
Present genitals	sexual		<i>Schlagintention</i> [hit intention] (Jantschke, 1972)	Hit away (?) (Rijksen, 1978)	walking
Present object	play		<i>Object vorzeigen</i> [present object] (Becker, 1988, Jantschke, 1972)	Presenting (Rijksen, 1978)	sexual behavior
Wave arm	play			Self decorate (Rijksen, 1978)	play
Facial expressions				Arm (leg) waving (MacKinnon, 1974)	intimidation/agonism
Grin	affiliation, agonistic, submissive			Arm wave (Rijksen, 1978)	play
				Fear face (MacKinnon, 1974)	agonism/fear
				Horizontal bared teeth face (Rijksen, 1978)	submission, fear
Open mouth	agonistic, play		Open mouth (Maple, 1980)	Bare-teeth threat (MacKinnon, 1974)	agonism/threatening
				Open mouth bared teeth face (Rijksen, 1978)	appeasement during play
Pout face	ingestion, parental care, affiliation		Funnel face (Maple, 1980)	Pout face (MacKinnon, 1974)	fear
				Pout moan face (Rijksen, 1978)	distress
				Silent-pout face (Rijksen, 1978)	submission, appeasement

Table 3. (continued)

Protruded lips	parental care, ingestion, submissive play	Playface (Maple, 1980)	play	Playface (MacKinnon, 1974)	play
Relaxed open mouth		<i>Spielgesicht</i> [play face] (Becker, 1984)	play	Relaxed open mouth (Rijksen, 1978)	play
Actions					
Bite	agonistic, ingestion, play, sexual	<i>Beißen</i> [Bite] (Becker, 1988)	play		
Chase	access, agonistic, ingestion, play	Biting, mouth biting (Zucker et al., 1978) <i>Spiellaufen</i> [play walk] (?) (Becker, 1988, Jantschke, 1972)	play	Loutish approach (?) (Rijksen, 1978)	play
Jump at	agonistic, play	<i>Anspringen, Fallenlassen</i> [[jump at] (Becker, 1988)	play		
Rock	agonistic, play			Body shake (MacKinnon, 1974)	intimidation/agonism
Swing	agonistic, play	<i>Strampeln</i> [struggle] (Becker, 1988)	play		
Walk backwards	play	<i>Scheinflucht</i> [Pretend escape] (Becker, 1988, Jantschke, 1972)	play		
Wrestle/Wrestle headfirst	agonistic, play	Dangling-hitting, wrestle (Maple, 1980)	play	Gnaw-wrestle (Rijksen, 1978) Wrestle (Rijksen, 1978, MacKinnon, 1974)	play agonism

hand directed upwards was only produced by one individual (*Lea*) to request food from another individual. Although the possibility that her being raised by humans altered her gestural repertoire can't be excluded, this gesture (*hand to mouth*) has also been seen in wild orangutans preceding *mouth-mouth contact* (Rijksen, 1978).

With respect to actions, wild young orangutans *wrestle*, *bite* or *grapple* to initiate play as well as they *chase* each other or *swing* to and fro using lianas (MacKinnon, 1974). A *loutish approach* is observed in both wild and captive orangutans as a "preceding meta-communication" to initiate play (Rijksen, 1978; Jantschke, 1972). Becker (1984) describes a behavior ("*Scheinflucht*") resembling 'walk backwards' of the present study and also refers to conspicuous movements produced in front of the social partner such as *somersaults*, *swinging* or *rolling* on the floor. Rijksen (1978) observed different variations of wrestling (*gnaw wrestling*, *hand wrestling*) in playful and agonistic interactions. A stereotypic rocking behavior is sometimes described in rehabilitant individuals as an attempt to attract a human's attention or to express frustration (Rijksen, 1978) and should not be confused with 'rock' of the current study.

The 'open mouth' facial expression of the present study is equivalent to the *bare-teeth threat* or *open mouth bared-teeth face* of wild orangutans (MacKinnon, 1974; Rijksen, 1978). The 'pout face' is also described for wild orangutans used in the context of mild fear (*pout moan face*, Rijksen, 1978; MacKinnon, 1974). MacKinnon (1974) refers to a *fear face* possibly resembling the 'grin' expression of the present study. The 'relaxed open mouth' is also known from wild orangutans (*play-face*, MacKinnon, 1974; Rijksen, 1978) functioning as a "meta-communicative signal" to initiate play. The 'protruded lips' expression resembles the *silent-pout face* described by Rijksen (1978) used as a submissive request for tolerance or appeasement as it was observed in the present study.

Functional context

Individuals used the majority of signals (33%) in the context of play. 25% of the time signals were used in the context of ingestion followed by 19% of signals used in an agonistic context and 8% in the context of affiliation. All other functional contexts were represented less than 5% of the time (Figure 1) with the lowest median percentage of signals used in the context of parental care (1.7%) and grooming (1.1%). Some signals were also observed in the context of submissive behavior or as a request to walk; however, those contexts are not considered in Figure 1, since interactions in those contexts were rare resulting

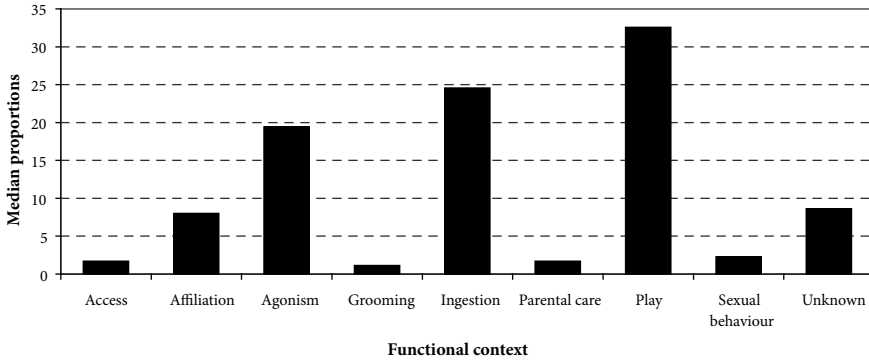


Figure 1. Median proportions of signals used across the different functional contexts.

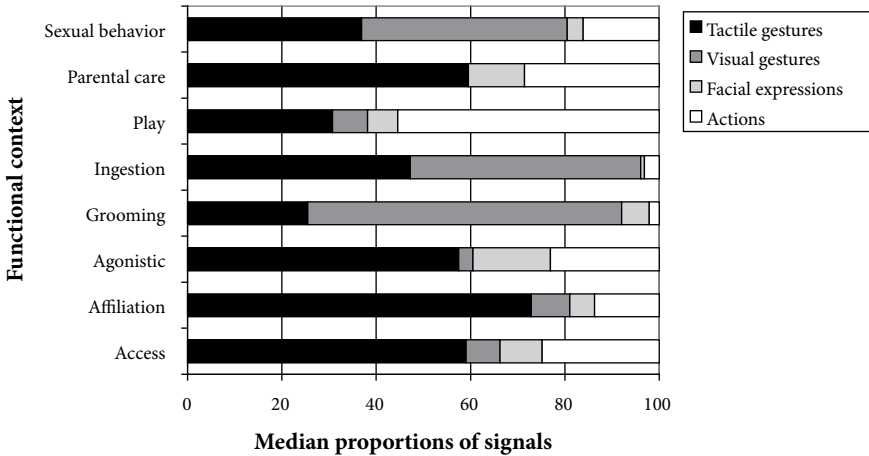


Figure 2. Median proportions of signal categories used across the different functional contexts.

in a median proportion of 0. In 8.6% of the time a particular context could not be determined.

Tactile gestures were the most frequent signal category that individuals used in the context of affiliative behavior ($\bar{x} = 72.9\%$), parental care ($\bar{x} = 59.5\%$), access ($\bar{x} = 59.1\%$), and agonistic behavior ($\bar{x} = 57.5\%$). Visual gestures dominated in the context of grooming ($\bar{x} = 72.5\%$), ingestion ($\bar{x} = 48.3\%$) and sexual behavior (45.3%), but were not used within the context of parental care. 11.9% of interactions within parental care were mediated by facial expressions which were also frequently observed within agonistic behavior ($\bar{x} = 11.1\%$). Actions

played a major role in the play context where 55.4% of all play bouts were initiated by this signal category (Figure 2).

Response to signals

The median proportion of response to signals was 59.6%. Considering signal categories, recipients responded in particular towards actions ($\bar{x} = 77.8\%$) and tactile gestures ($\bar{x} = 61\%$), but only 55.6% of the time towards facial expressions and even less to visual gestures ($\bar{x} = 33.3\%$). Thus, when analyzing the response types depending on functional context, the lowest proportion of response was observed in the context of ingestion ($\bar{x} = 43.8\%$), whereas the highest was in the contexts of access ($\bar{x} = 78.3\%$) and grooming ($\bar{x} = 71.3\%$).

Sender-recipient interactions

From all the interactions observed within a group the majority took place between dyads of subadults and/or the juvenile individual (Leipzig: 16.9%; Zuerich: subadult and juvenile 26.7%; 19.7% subadult and subadult), whereas interactions within an adult dyad occurred least often (Leipzig: 2.58%, Zuerich: 3.7%).

Considering functional contexts, most interactions in play situations occurred within dyads of young individuals in both groups. Interactions between two adults in the play context were absent in Leipzig and only less than 1% of playful interactions occurred between adult dyads in Zuerich group, namely the two males. In the context of ingestion, most interactions in Leipzig group took place between the subadult individual and its mother (32.4%) with the subadult acting as sender. Adults were recipients of signals in this context in 65.7% (Leipzig) and 68.1% (Zuerich), of the time, respectively, but interactions in this context occurred also between adults (Leipzig: 15.6%; Zuerich: 10.4%). In the agonistic context, adults of both groups most often acted as senders towards the subadult and juvenile individuals, whereas agonistic interactions between adults were rare (Leipzig: 2.7%, Zuerich: 5.9%).

Variability of the signal repertoire

The signals observed were analyzed with regard to individual differences in the number and frequency of signals used as a function of groups, age classes, or sex.

Individual differences

Table 4 shows the distribution of all signals among individuals and the total number of signals for each individual. None of the orangutans used all of those signals; the individual numbers ranged from seven (*Bimbo*) through 31 signals (*Toba*) with a median of 21 signals (corresponding to 47.7% of the total number of signals observed). Table 4 also shows for each signal the percentages of individuals that performed it. Four signals, including two tactile gestures ('put hand on head', 'hold hand in front of the mouth'), one visual gesture ('jerking body movements') and one action ('box'), were each used by only one individual. Only two tactile gestures ('slap', 'push') were used by all 16 individuals and 'pull' and 'gentle touch' were performed by all individuals except *Bimbo*. Significant differences were found between the number of signals used depending on the signal category (Friedman test: $\chi^2 = 35.06$, $df = 3$, $p < 0.001$): Individuals performed a higher variety of tactile gestures ($\bar{x} = 8$) compared to visual gestures ($\bar{x} = 6$), facial expressions ($\bar{x} = 1$) and actions ($\bar{x} = 4$). Furthermore, a higher number of visual gestures and actions was used compared to the number of facial expressions (Wilcoxon test: tactile gestures versus visual gestures: $Z = -2.887$, $p = 0.004$, $N = 12$; tactile gestures versus facial expressions: $Z = -3.531$, $p = 0.004$, $N = 16$; tactile gestures versus actions: $Z = -3.193$, $p < 0.001$, $N = 13$; visual gestures versus facial expressions: $Z = -3.311$, $p < 0.001$, $N = 14$; visual gestures versus actions: $Z = -1.957$, $p = 0.063$, $N = 12$, facial expressions versus actions: $Z = -2.964$, $p = 0.004$, $N = 15$).

Group differences

Nine signals were observed in only one of the two groups (see Table 3). The majority of those signals were used by only two or three individuals per group, whereas 'bite in hand' and 'embrace' were performed by the majority of individuals of the Leipzig group and therefore might be considered as 'group specific' gestures (Pika et al., 2003). The 'offer arm with food pieces' may represent another example of a group specific gesture, although only three out of seven individuals used it. However, none of those signals was used by all members of one particular group.

To analyze whether the signal repertoire was more uniform within each group than between the two groups a Cohen's kappa was calculated. The within group kappa of the Zuerich group was 0.53 and 0.54 for the Leipzig group representing a 'moderate' level of agreement (Altman, 1991). Thus, the variability of the individual repertoires within each group was approximately the same in

Table 4. Distribution of signals among individuals. The percentages of individuals using each signal are shown together with some specific remarks on the identity of the individuals and distribution of signals across the two groups, respectively, as well as the total of signals used by each individual. The individuals are ordered according to their group affiliation and within each group with decreasing age. Age classes refer to adults (A), subadults (S), juveniles (J), and infantile (I). Males are marked in bold letters.

Signals	Group		Zuerich										Leipzig					% of individuals	Remarks		
	Age class	Individuals	A					S	J	A					S	J	I				
			Pongo	Lea	Timor	Selatan	Oceh	Djaro	Salih	Tuah	Xira	Dunja	Bimbo	Pini	Walter	Toba	Padana			Kila	
1. Tactile gestures																					
Bite in hand	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	X	X	-	25	only Leipzig group
Embrace	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	X	X	-	25	only Leipzig group
Formal bite	X	X	X	X	X	X	X	X	X	X	X	X	X	-	X	X	X	X	-	88	all except Bimbo and Kila
Gentle touch	X	X	X	X	X	X	X	X	X	X	X	X	X	-	X	X	X	X	X	94	all except Bimbo
Hold tight	X	X	-	-	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	31	in both groups
Lip touch	X	X	-	X	X	X	X	X	X	X	X	X	-	X	X	X	X	X	X	88	in both groups
Nudge	X	X	X	X	-	-	X	X	X	X	X	X	X	X	X	X	X	X	X	88	all except Oceh and Djaro
Pull	X	X	X	X	X	X	X	X	X	X	X	X	X	-	X	X	X	X	X	94	all except Bimbo
Push	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100	all
Put face on face	X	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	13	only Zuerich group (males)
Put hand on head	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	Lea (Zuerich)
Slap	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100	all
Throw object	-	X	-	-	-	-	X	-	X	-	-	-	-	-	-	-	-	-	-	19	only Zuerich group
Touch with genital region	-	-	-	-	X	-	X	-	-	-	-	-	X	-	X	-	-	-	-	25	in both groups
2. Visual gestures																					
Approach the face	-	X	X	X	X	X	X	X	X	-	-	X	X	X	X	X	X	X	X	81	in both groups
Bite intention	X	-	-	X	X	X	X	-	-	X	-	X	X	X	X	-	-	-	-	63	both groups
Extend arm	-	-	-	X	X	-	X	X	X	X	X	X	X	-	X	X	X	-	-	69	in both groups
Offer arm with food pieces	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	-	-	19	only Leipzig group
Hand shake	-	-	-	X	-	X	X	X	-	-	X	X	X	-	-	-	-	-	-	38	in both groups
Headstand	-	-	-	-	-	-	-	-	-	-	X	-	-	X	-	-	-	-	-	13	only Leipzig group
Hit intention	X	-	X	X	-	-	X	X	-	-	X	-	-	X	-	-	X	-	-	44	in both groups
Hold hand in front of the mouth	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	Lea (Zuerich)

Table 4. (continued)

Jerking body movements	- - - - - X - - - - - - - - -	6	Salih (Zuerich)
Offer body part	- - - X X - X - X - - - - - X X	38	in both groups
Offer food	- X - - - - - X X - - - X X X -	38	in both groups
Present genitals	- X - - X - X X X - - - - X X -	44	in both groups
Present object	- X X - - - - X - - - - - X -	25	three of Zuerich group
Shake object	- - - - X - X X X - X X X X X -	56	in both groups
Wave arm	- - - X - - - - X - - - - - - -	13	only Zuerich group
3. Facial expressions			
Grin	- - - - X X X - - - - - X X -	31	both groups
Open mouth	X X X X X X - X X - X X X X -	75	both groups
Playface	X X - - - - - X - - - - - - -	19	only Zuerich group
Poutface	- - - - - - - X - - - - - X	13	both groups, young individuals
Protruded lips	- X - - X - - - - - - X - -	19	
4. Actions			
Bite	X X X X X - X X X X - X X X X X	88	both groups
Box	- - - - - - - - - - - X - -	6	Toba (Leipzig)
Chase	- - X X X - X X X - - X X X X -	63	both groups
Jump at	- - - - X X X X X - - - X X X -	50	both groups
Rock	- - - - - - - - - - - X X X	19	only Leipzig group
Swing	- - - - - X X X X - - - X X X X	50	both groups
Swing headfirst	- - - - - - X X - - - X X X -	33	both groups
Walk backwards	- - - - - - X X - - - X - - -	19	both groups
Wrestle headfirst	- - - X - - X X X - - X - X X X	50	both groups
Wrestle-biting	X X - X X X X X X X - X X X X X	88	both groups
<i>Total of signals</i>	15 20 12 18 21 14 25 25 28 14 7 21 21 31 28 15		

both groups (Mann-Whitney U-test: $U = 28$, $p = 0.76$, $n_{\text{Zuerich}} = 9$, $n_{\text{Leipzig}} = 7$). The between group kappa was 0.51 representing a slightly higher degree of variability between the individual repertoires of the two groups, but this difference was not significant (Wilcoxon-test: $Z = -1.500$, $p = 0.134$, $N = 16$). These results suggest that despite the fact that the general concordance of the individual's repertoires was only 'moderate', the variability of those repertoires was the same both within and between groups.

Age differences

Qualitatively, there were no distinct differences between the signals used by young and adult orangutans. 'Put face to face' and 'put hand on head' were tac-

tile gestures only performed by adults as well as the visual gesture 'hold hand in front of the mouth', but each of those gestures was used mostly by single individuals. The same was true for 'box' and 'jerking body movements', where only one single subadult used each of them. The facial expression 'pout face' was only observed in one juvenile and the one infant, whereas the action 'rock' was used by all young orangutans of the Leipzig group (see Table 4).

There was a negative correlation between the total number of signals used and age class (Spearman's correlation: $r_s = -0.608$, $p = 0.013$, $N = 16$). The median number of signals performed increased from 15 in the infantile individual to 28 in juveniles and 25 in subadult individuals, but dropped to 17 in adult orangutans. Subadults performed a significantly larger number of signals than adults (Kruskal-Wallis test: $\chi^2 = 9.945$, $df = 3$, $p = 0.001$; $N = 16$; Mann-Whitney U-test: subadult versus adults: $U = 0$, $p = 0.018$, $n_{\text{subadult}} = 3$, $n_{\text{adult}} = 10$; all other p -values ≥ 0.15). With respect to the different signal categories, Figure 3a shows the median number of tactile and visual gestures, facial expressions and actions used by each age class. Both juveniles and subadults performed a higher number of visual gestures ($\bar{x}_{\text{juveniles}} = 9$, $\bar{x}_{\text{subadult}} = 8$) and actions ($\bar{x}_{\text{juveniles}} = 8$, $\bar{x}_{\text{subadult}} = 8$) compared to adult orangutans, (visual gestures: $\bar{x} = 4$; actions: $\bar{x} = 2.5$), but significant differences were only found between subadults and adults. There was also a trend that juveniles used a higher number of actions compared to adults and that both juveniles and subadults performed a higher number of visual gestures than adult orangutans (Mann-Whitney U-test: for actions: subadults versus adults: $U = 1$, $p = 0.042$, $n_{\text{subadult}} = 3$, $n_{\text{adult}} = 10$, juveniles versus adults: $U = 0$, $p = 0.075$; for visual gestures: juveniles versus adults: $U = 0$; $p = 0.075$, $n_{\text{juvenile}} = 2$, $n_{\text{adult}} = 10$, subadults versus adults: $U = 1$, $p = 0.075$, $n_{\text{subadult}} = 3$, $n_{\text{adult}} = 10$).

However, although young orangutans used a wider repertoire of signals, the analysis of the degree of concordance of the individual repertoires within age classes found that the repertoires of young orangutans showed a higher degree of concordance ($\kappa = 0.68$) than the repertoires of adults (0.51) (Mann-Whitney U-test: $U = 0$, $p < 0.001$, $n_{\text{youngsters}} = 6$, $n_{\text{adult}} = 10$) which was a significant difference.

In terms of frequency, there was an increase in the proportion of tactile gestures used with age (from 29.13% of the infant to a median proportion of 54.5% in adults). Adults also produced facial expressions more frequently (12%) than young orangutans (1.4%–3.1%) (Figure 3b). However, those differences were not significant after correcting them for multiple testing using Bonferroni-Hochberg method (all p -values ≥ 0.12).

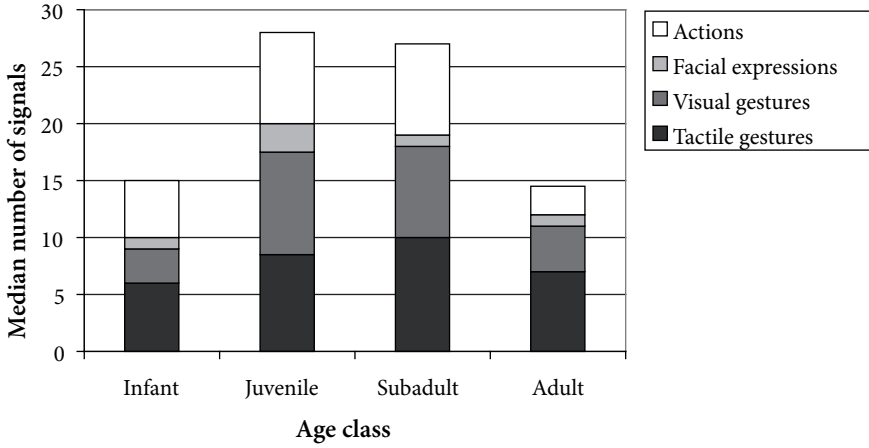


Figure 3a. Median number of signals depending on signal categories shown for each age class.

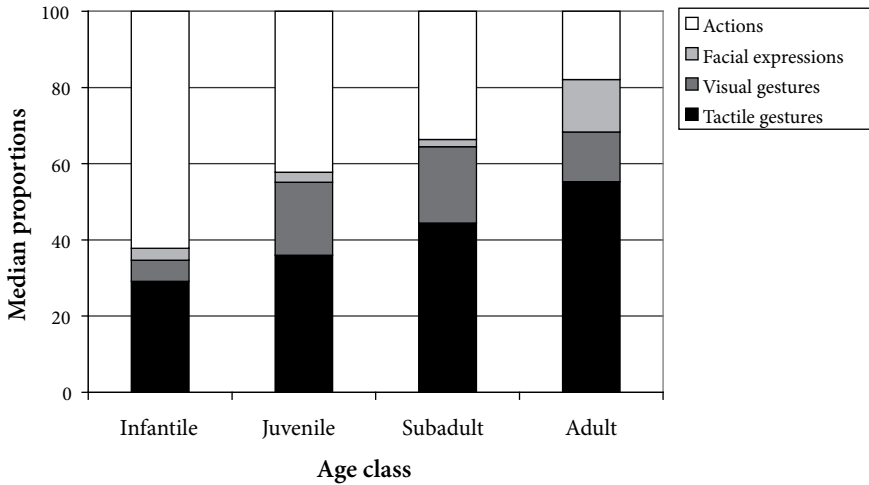


Figure 3b. Median proportion of signals depending on signal categories shown for each age class.

Sex differences

Only adult males were available in the two groups as opposed to females which represented all age classes. Thus, the sample size for both adult males and females was rather small. Thus, only adult females were compared with the (adult) males. The median number of signals used by the adult males was 14.5 and 19.5 signals for females. No significant differences were found between

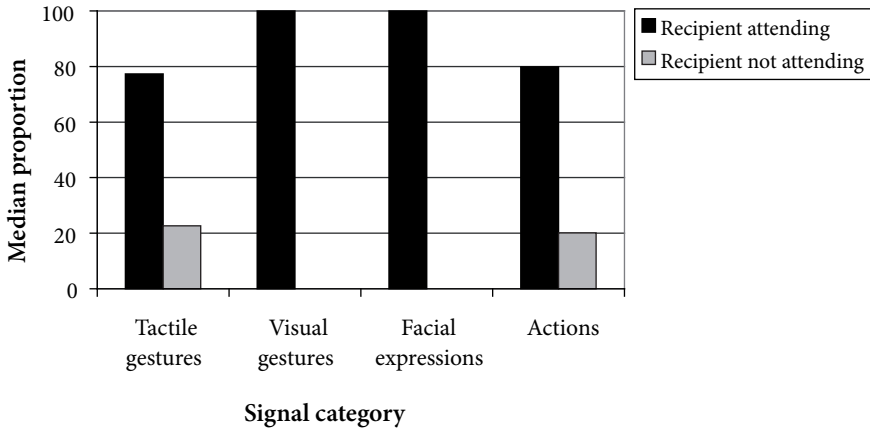


Figure 4. Median proportions of signals used towards an attending and not attending recipient, respectively depending on signal category.

the sexes with respect to the total number of signals used as well as for the different signal categories (Mann-Whitney U-test: total: $U = 8$, $p = 0.48$; tactile gestures: $U = 7$, $p = 0.362$; visual gestures: $U = 6$, $p = 0.238$; facial expressions: $U = 10$, $p = 0.662$; actions: $U = 10.5$, $p = 0.729$, $n_{\text{males}} = 4$, $n_{\text{females}} = 6$).

Flexibility

Attentional state

Visual gestures and facial expressions were virtually never used in case the recipient was not attending (Figure 4). All four signal categories were used significantly more often towards an attending recipient than to one not attending (Wilcoxon-test: tactile gestures attending versus not attending: $Z = -3.516$, $p < 0.001$, $N = 16$; visual gestures attending versus not attending: $Z = -3.653$, $p < 0.001$, $N = 16$; facial expressions attending versus not attending: $Z = -3.564$, $p < 0.001$, $N = 16$; actions attending versus not attending: $Z = -3.238$, $p < 0.001$, $N = 15$), but visual gestures were used significantly more often towards an attending recipient than tactile gestures and actions (Friedman test: $\chi^2 = 14.688$, $df = 3$, $p = 0.001$; Wilcoxon-test: visual gestures versus tactile gestures: $Z = -3.4077$, $p = 0.001$, $N = 15$; visual gestures versus actions: $Z = -3.107$, $p = 0.002$, $N = 14$).

One signal in several functional contexts

Overall, 81.8% ($N = 36$) of the total number of signals were observed in more than one functional context, whereas nine signals were used for only one

Table 5. Means-end dissociation: Use of one signal in the different functional contexts and all signals used within each of the function contexts.

	Access	Affiliation	Agonistic	Grooming	Ingestion	Parental care	Play	Sexual behavior	Submissive behavior	Walk	Sum of contexts
Tactile gestures											
Bite in hand		X			X		X				3
Embrace		X				X					2
Formal bite	X		X	X	X	X	X	X			7
Gentle touch	X	X	X	X	X	X	X	X		X	9
Hold tight		X	X				X				3
Lip touch	X	X		X	X		X				5
Nudge	X	X	X		X	X	X				6
Pull	X	X	X	X	X	X	X	X		X	9
Push	X	X	X	X	X	X	X	X			8
Put face on face		X					X				2
Put hand on head		X	X								2
Slap	X		X		X		X	X			5
Throw object		X					X				2
Touch with genital region		X	X					X			3
Visual gestures											
Approach face	X	X		X	X						4
Bite intention			X	X	X		X	X			5
Extend arm		X			X		X				3
Headstand		X					X				2
Hit intention			X				X				2
Hold hand in front of the mouth					X						1
Jerking body movements								X			1
Offer arm with food pieces					X						1
Offer body part				X							1
Offer food			X		X						2
Present genitals								X			1
Present object		X					X				2
Shake hands			X		X		X	X			4
Shake object			X				X				2
Wave arm							X				1
Facial expressions											
Grin	X	X	X			X			X		5
Open mouth	X		X		X		X	X			5
Relaxed open mouth							X				1
Pout face		X			X	X					3
Protruded lips		X	X				X		X		4

Table 5. (continued)

	Access	Affiliation	Agonistic	Grooming	Ingestion	Parental care	Play	Sexual behavior	Submissive behavior	Walk	Sum of contexts
Actions											
Bite			X	X	X	X	X	X			6
Box	X	X			X	X					4
Chase	X		X		X		X	X			5
Jump at	X		X		X		X	X			5
Rock			X				X				2
Swing		X	X				X				3
Swing headfirst	X						X				2
Walk backwards							X				1
Wrestle	X	X	X		X		X	X			6
Wrestle headfirst		X	X		X		X				4
Sum of signals	15	23	24	9	23	10	31	15	2	2	

functional context with the majority representing visual signals (18.1%, $N=8$) (Table 5). For example, 'offer body part' was only observed in the context of grooming, 'jerking body movements' and 'present genitals' in the sexual context, 'wave arm' exclusively during play, 'offer arm with food pieces' and 'hold hand in front of the mouth' in the context of ingestion.

With respect to the individual use of one signal in different contexts, visual gestures were used in a significantly lower number of functional contexts ($\bar{x}=1$) than tactile gestures ($\bar{x}=1.5$), facial expressions ($\bar{x}=1.6$) and actions ($\bar{x}=1.4$) (Kruskal-Wallis-test: $\chi^2=11.78$, $df=3$, $p=0.008$; Mann-Whitney U-test: for visual gestures versus tactile gestures: $Z=-2.941$, $p=0.003$; for visual gestures versus facial expressions: $Z=-2.545$, $p=0.01$; for visual gestures versus actions: $Z=-2.463$, $p=0.0019$).

One functional context with several signals

Overall, the highest variety of signals was used in the play context ($N=31$, 70.5%) followed by agonistic behavior ($N=24$, 54.5%). 52.3% ($N=23$) of all signals were used for affiliation and ingestion, respectively, and 34.9% ($N=15$) were observed within sexual behavior and the context of access. 22.7% ($N=10$) of the signals occurred with in parental care and 20.5% within grooming. Only

4.5% ($N=2$) of all signals were used within submissive behavior and walk, respectively (Table 5).

Considering individuals' performance, then for 75% of all functional contexts more than one signal ($\bar{x}=3.8$ per context) was used. The highest number of signals was used within ingestion ($\bar{x}=11.5$) which was a significantly higher number of signals compared to all other contexts except play and agonistic behavior ($\bar{x}=8.5$ in both contexts) (Friedman test: $\chi^2=89.75$, $df=9$, $p<0.001$; Wilcoxon-test: ingestion compared to each other context: all p -values ≤ 0.029 except for comparison with play: $Z=-0.441$, $p=0.66$, $N=14$; and agonistic behavior: $Z=-1.766$, $p=0.077$, $N=15$).

In terms of signal category, individuals used a median of 1.9 different tactile gestures, 0.8 visual gestures, 0.3 facial expressions and 0.8 actions per context. The highest variety of tactile gestures was observed in the agonistic context ($\bar{x}=3.9$) followed by the play context ($\bar{x}=3.3$). The highest number of visual gestures was also used in the agonistic context ($\bar{x}=1.9$) followed by 1.8 visual gestures used in the context of ingestion and play. The highest variety of facial expressions occurred in the agonistic context and play, respectively ($\bar{x}=0.8$) and a median of 3.9 actions was used in the play context.

Signal sequences

Approximately 22.1% ($N=467$) of all observed signals were combined in one of 178 signal sequences. Figure 5 shows the proportion of sequences as a function of the number of signals combined. The majority (65.7%) represented two signal sequences; the proportions of the other various signal sequences declined steadily as the number of signals in a sequence increased. The highest number of signals performed one after another was 10, which was observed only once. The median number of gesture sequences per individual was 8.5; one individual (*Bimbo*) never combined two or more signals one after another. Most of the sequences occurred within the functional contexts of play ($N=80$, $\bar{x}=44.4\%$), whereas no signal combination was observed within the context of grooming.

Overall, 52.5% ($N=93$) of the sequences were repetitions of the same signal, most of them tactile gestures (72%). In 23.7% of all repetitions the same signal was repeated more than once. With respect to components of signal sequences, tactile gestures represented the biggest proportion within sequences (58.5%), followed by actions (25.1%), visual gestures (10.1%) and facial expressions (2.4%) resembling the findings of the general frequency distribution of signals.

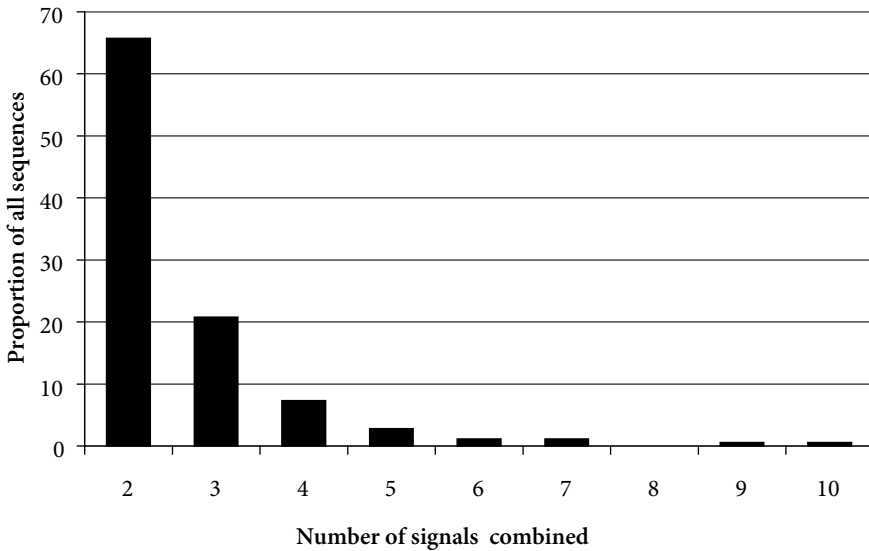


Figure 5. Proportion of signal sequences as a function of the number of signals combined

With respect to the response toward the first signal, the attentional state before the first signal and the response type afterwards were analyzed. The recipient did not respond in 70.1% of the sequences, where both the attentional state and the response of the recipient were known ($N = 154$). Therefore, signal sequences seemed to emerge because of the lack of response from the recipient.

Discussion

The current study systematically documents the individual use of signals in orangutans as a function of group, age class and sex with focus on the intentional and flexible use of signals in different functional contexts.

The main findings are that orangutans use a considerable number of signals including tactile and visual gestures as well as several more complex actions, but few facial expressions. No auditory gestures were produced. One third of signals occurred within the play context followed by one fourth in the context of ingestion. Almost half of the signals produced were tactile gestures and they were used most often in the contexts of affiliation and agonism, whereas visual gestures dominated in the contexts of grooming, ingestion and sexual behavior.

Actions frequently occurred in the context of play, whereas facial expressions were used particularly within parental care and agonistic behavior.

The comparison of the signals observed in the current study with other publications on gestures and facial expressions of orangutans showed that the majority of the signals were also found among wild and other captive individuals and therefore seem to represent typical components of orangutans' communicative repertoire. However, nothing could be found in the literature in regard to the gestures 'offer body part' or an active invitation to share food such as 'offer food' or 'extend arm with food pieces'. Of course, this sort of signal could be present in orangutans and may have been missed by previous studies because of inadequate observation conditions. For example, the observations of Maple (1980), Zucker, Mitchell, and Maple (1978), and Becker (1984) focused on the play behavior of orangutans but other functional contexts were not considered. Maple (1980) also mentions two auditory gestures such as *clapping* and *pounding chest*. However, since he observed them prior to feeding time in a captive setting those gestures might be related to interactions with humans rather than conspecifics, and these kinds of interactions were not considered in the current study.

In terms of variability, differences in the use of signals as a function of group, age, and sex were identified. Individuals utilized a higher variety of tactile gestures compared to all other signal categories, which is similar to findings for gorillas, bonobos and siamangs (Pika et al., 2003; Pika et al., 2005; Liebal et al., 2004). Some of the signals were produced by only one individual (*Lea*) such as 'put hand on the head' which she used to calm the juvenile after agonistic encounters with other group members. It is difficult to define those cases as idiosyncratic signals since the occurrence of one particular signal in only one individual can often explained by social factors, housing conditions or even rearing history. For example, the action 'box' was used by only one subadult individual to get access to the milk of its mother who mostly refused because she already had another offspring. However, since no other individual was weaned during the course of observation, it is very likely that this signal may occur between other offspring-mother dyads under different social conditions.

With respect to group differences, there were some signals observed in only one group, such as 'bite in hand', 'embrace' or 'offer arm with food pieces'. However, since only some of the individuals within one group used these signals, it is difficult to define them as 'group specific' signals according to Pika et al. (2003), saying that "a group specific signal has to be observed in the majority of individuals of different generations within one group". A problem in this regard is that the observation period might have been too short and therefore it

is very likely that some signals did not occur during this time. For example, the gesture 'embrace' was not observed in the Zuerich group, but has been reported in other studies (Rijksen, 1978; MacKinnon, 1974) and therefore seems to be a common gesture of orangutans. Another interesting example is the 'offer arm with food pieces' only observed in the Leipzig group, although the diet of both groups consisted of leaves and other greens which could have been chewed into the fur. Therefore, although this gesture was produced by only three individuals in the Leipzig group, this behavior might represent a case for a 'group specific' gesture since its occurrence can't be explained by either social or housing conditions.

Individual signal repertoires showed a remarkable degree of variability with respect to the kind of signals used by each individual, but the variability of the signal repertoires within the group was the same as the variability between groups. When comparing these results with other ape species, the individual repertoires of orangutans show a similar degree of variability to that of bonobos, whereas chimpanzees' repertoires were the most variable (Tomasello et al., 1997; Pika et al., 2005). In contrast, the individual repertoires of siamangs and gorillas are characterized by a higher degree of concordance (Liebal et al., 2004; Pika et al., 2003). Pika (2002) argues that the cohesiveness of the gorilla's social system causes the uniform character of individual repertoires, which would also apply to siamangs because of their small, stable family groups characterized by strong bonding between the adult male and female (Chivers, 1976; Fischer & Geissmann, 1990). In contrast, the fission-fusion society of bonobos and chimpanzees is characterized by a high degree of variability and changeableness (Nishida, 1979; Wrangham & Smuts, 1980; Thompson-Handler, Malenky, & Badrian, 1984; Fruth & Hohmann, 2002) resulting in a variable and flexibly used communicative repertoire (Tomasello et al., 1994, 1997; Pika et al., 2005). The current results regarding the orangutans' variability of individual signal repertoires seem to fit into this pattern, since they also live in a variable individual-based fission-fusion system (Delgado & van Schaik, 2000).

In terms of variability between age classes, the total number of signals used increased with age but dropped in adults, resembling findings for other ape species such as siamangs and chimpanzees (Tomasello et al., 1997; Liebal et al., 2004). Young gorillas peak in the number of gestures performed at the age of 2–3 years, which might be explained by their rather short maturation period compared to other great ape species (Pika et al., 2003). Qualitatively, there were no signals that were used exclusively by either young or adult orangutans, but the variety and frequency of signals changed depending on the functional contexts they were used for. Young orangutans used a higher number of visual ges-

tures and actions compared to adults to initiate play, whereas adults only rarely engaged in this functional context. In contrast, adults engaged more often in agonistic encounters or sexual interactions using particular signals which were not used by their offspring in those contexts. Thus, it was not the case that adults used different signals than young orangutans, but the age classes were distinguished by using the same signals in different functional contexts.

The analysis of the variability of signal repertoires depending on the sex of the sender was restricted since only four males that were all adult individuals were observed in this study. Overall, females used a higher number of signals, but this result may be because fully-developed, flanged males only rarely interacted with other group members in this study, resembling findings in wild orangutans (Delgado & van Schaik, 2000; Rijksen, 1978; MacKinnon, 1974).

In terms of the flexible use of the different signal categories, orangutans performed visual-based signals such as visual gestures and facial expressions only if the recipient was attending. This is consistent with findings for other great ape species as well as siamangs who virtually never use visual signals when a recipient is not attending (Pika et al., 2003, 2005; Tomasello et al., 1997; Liebal et al., 2004). Orangutans produced the majority of signals in more than one functional context as well as they used a variety of different signals to communicate a specific social goal within one functional context. This suggests that the signals were used in a flexible way and do not represent stereotyped behavior linked to a particular social context. As with siamangs and other great ape species (Liebal et al., 2004; Pika et al., 2003, 2005), tactile gestures represented the most flexibly used signal category, whereas the highest variety of signals was observed in the play context. However, orangutans also used a remarkable number of signals in the context of ingestion. Interactions in this context were also not restricted to mother-offspring dyads but the majority of signals were directed from a younger or subdominant individual towards the older or higher-ranking one (Rijksen, 1978).

Signal sequences may also represent a method to increase the flexibility of a signal repertoire consisting of a limited number of components. These combinations may enable the sender to consider previous interactions with a particular recipient and to adjust the signal depending on the recipient's state of attention as well as to force a response by repeating or substituting signals. The orangutans in the present study frequently combined signals, mostly in two signal sequences and most often in the context of play. Approximately half of the sequences were repetitions of the same signal, with tactile gestures being the most frequent signal category combined. Signal sequences seemed to emerge in particular because of the lack of a response in 70% of all sequences

compared to only 40% to single signals. These results again resemble findings for siamangs and chimpanzees with respect to the type and number of signals combined as well as the emergence of signal sequence because the recipient did not respond, although the proportion of signals sequences was slightly lower in orangutans (22% compared to approx. 30% in siamangs and chimpanzees) (Liebal, Call, & Tomsello, 2004; Liebal et al., 2004; Tomasello et al., 1994).

The social system of orangutans is comparable to the fission–fusion system of chimpanzees (Delgado & van Schaik, 2000) and this structure seems to be the major force selecting for a highly variable communicative repertoire of gestures, actions and facial expressions used flexibly in a number of different functional contexts (Maestriperieri, 1999). The high degree of variability found in the present study supports this hypothesis. However, as opposed to chimpanzees, both wild and captive adult orangutans usually tolerate each other but do not seek the contact with other individuals and no particular greeting gestures are reported (MacKinnon, 1974; Galdikas & Vasey, 1992; Jantschke, 1972). Rijksen (1978) mentions that play bouts only occur between young individuals, but not between adults. This is also supported by the findings of the present study. Interactions between adults were rare, even in the agonistic context, and the majority of playful interactions was observed between subadult and juvenile individuals.

Maestriperieri (1999) proposed that if there is any evolutionary trend in communicative systems it should be pronounced by an increase of complexity of the signals. However, it is difficult to define and measure the complexity of a particular signal or a repertoire of a species, since complexity is not simply constituted by the number of signals used. One aspect reflecting the cognitive skills of a species might be the use of objects within communicative interactions (Chevalier-Skolnikoff, 1976). In contrast to siamangs (Liebal et al., 2004), both wild and captive orangutans incorporated objects into their production of gestures, such as throwing objects, slapping with sticks, shaking branches or other objects or presenting an object (MacKinnon, 1974; Rijksen, 1978; Maple, 1980). Furthermore, many of their signals were manual gestures rather than body postures and facial expressions, which are used more frequently in monkey species such as macaques and baboons (Hinde & Rowell 1962; Kummer & Kurt, 1965) as well as in siamangs (Liebal et al., 2004). This clearly differentiates orangutans' signal repertoire from that of monkeys and siamangs and is more similar to the signal repertoires of other great ape species. Similar to the African great ape species (Tomasello et al., 1997; Pika et al., 2003, 2005), orangutans performed a higher variety of visual gestures than siamangs (Liebal et al., 2004). However, both siamangs and orangutans most frequently produced

tactile gestures, supporting the idea that arboreal species should mainly use tactile gestures rather than visual gestures because of the restricted range of vision in their habitat (Marler, 1965). An important constraint of this study is that the captive environment can't offer the same degree of structure, variability and size as it can be found in the field. Captive individuals are also limited in their choice of whom they would like to interact with, and the group composition does not necessarily reflect the social structure of wild populations. Furthermore, the sample size of young individuals was rather small and the comparison of males and females was limited to adult individuals. Therefore, the results presented here are representative for the two observed groups, but it is necessary to compare these findings with wild individuals to confirm that their communicative behavior follows the overall pattern observed in captivity.

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Authors' address

Katja Liebal
Department of Psychology
University of Portsmouth
Portsmouth
PO1 2DY
UK

E-mail: katja.liebal@port.ac.uk

About the authors

Katja Liebal, Diplom thesis in Biology in 2001 from University of Leipzig. PhD student at the Max Planck Institute of Evolutionary Anthropology, Leipzig, Germany with interest in comparative research of social communication in different ape species. Since April 2005 lecturer in the department of psychology, University of Portsmouth (UK).

Simone Pika, PhD in Biology in 2003 from Westfälische Wilhelms University Münster, Germany. Worked at the MPI for evolutionary Anthropology (D) from 1999–2003. Since October 2003 postdoctoral fellow in the department of Psychology, University of Alberta, Canada and currently working as a postdoctoral fellow at the University of St. Andrews, Scotland. Her research interest centres on the development and use of communicative signals of non-human and human primates with a special focus on processes of social cognition and the evolutionary roots of spoken language.

Michael Tomasello, PhD in Psychology in 1980 from University of Georgia (USA); taught at Emory University and worked at Yerkes Primate Center (USA) from 1980 to 1998; since 1998, Co-Director, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. Research interests focus on processes of social cognition, social learning, and communication in human children and great apes. Books include *Primate Cognition* (w. J. Call, Oxford University Press, 1997), *The New Psychology of Language: Cognitive and Functional Approaches to Language Structure* (edited, Erlbaum, 1998), *The Cultural Origins of Human Cognition* (Harvard University Press, 1999), *Constructing a Language: A Usage-Based Theory of Language Acquisition* (Harvard University Press, 2003).