RESEARCH ARTICLE

Gestural Communication in Subadult Bonobos (*Pan paniscus*): Repertoire and Use

SIMONE PIKA[1,3]*, KATJA LIEBAL[2], AND MICHAEL TOMASELLO[2]
[1]*Department of Psychology, University of Alberta, Edmonton, Canada*
[2]*Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*
[3]*Centre for Research and Conservation (CRC); Royal Zoological Society of Antwerp (RZSA), Belgium; and Zoo Apenheul, The Netherlands.*

This article aims to provide an inventory of the communicative gestures used by bonobos (*Pan paniscus*), based on observations of subadult bonobos and descriptions of gestural signals and similar behaviors in wild and captive bonobo groups. In addition, we focus on the underlying processes of social cognition, including learning mechanisms and flexibility of gesture use (such as adjustment to the attentional state of the recipient). The subjects were seven bonobos, aged 1–8 years, living in two different groups in captivity. Twenty distinct gestures (one auditory, eight tactile, and 11 visual) were recorded. We found individual differences and similar degrees of concordance of the gestural repertoires between and within groups, which provide evidence that ontogenetic ritualization is the main learning process involved. There is suggestive evidence, however, that some form of social learning may be responsible for the acquisition of special gestures. Overall, the present study establishes that the gestural repertoire of bonobos can be characterized as flexible and adapted to various communicative circumstances, including the attentional state of the recipient. Differences from and similarities to the other African ape species are discussed. Am. J. Primatol. 65:39–61, 2005. © 2005 Wiley-Liss, Inc.

Key words: gestural inventory; learning; use; flexibility; *Pan paniscus*

INTRODUCTION

Gesture: The use of motions of the limbs or body as a means of expression [Oxford English Dictionary].

The behavior of wild chimpanzee communities (*Pan troglodytes*) has been studied extensively [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1970], and these long-term studies provide evidence that gestural signaling plays an important role in chimpanzee communication. For instance, Goodall [1986]

(but see also Plooij [1978, 1979]) reported that wild chimpanzees in the Gombe National Park use more than a dozen distinct gestures in a variety of contexts, including play, agonistic behavior, and sex. In addition, gestural signals such as *leaf clipping* [Nishida, 1980] and *grooming hand clasp* [McGrew & Tutin, 1978] provide evidence for the existence of population-specific differences in the wild. The *leaf-clipping* gesture was observed at Mahale, Bossou, and Tai [Boesch, 1995; Nishida, 1980; Sugiyama, 1981]. Interestingly, this gestural signal was utilized in sexual, play, or frustration contexts at Mahale, mainly in play and frustration contexts at Bossou, and as a part of a drumming display by males at Tai.

Gestural communication has been investigated further in captive groups of chimpanzees [Tomasello et al., 1994, 1997; Van Hooff, 1973]. Tomasello and colleagues focused on the learning processes involved in the acquisition of gestures, and found no evidence that a social learning process was involved. Social learning has been defined as ''a group of learning mechanisms in which observation of other individuals facilitates or enables the acquisition of a novel behavior'' [Call, 1999, p 317]. Scientists tend to discriminate at least four main phenomena: social facilitation, local and stimulus enhancement, emulation, and imitation (for an overview see recent reviews by, e.g., Heyes [1994] and Whiten and Ham [1992]). Based on their findings, Tomasello and colleagues therefore suggested that the main learning process involved in the acquisition of gestures by chimpanzees is an individual learning process called ''ontogenetic ritualization.'' In ontogenetic ritualization, a communicatory signal is created by two individuals shaping each other's behavior in repeated instances of an interaction [Tomasello & Call, 1997]. Furthermore, Tomasello and colleagues [1994] showed that common chimpanzees accommodate their use of gestures to the attentional state of the recipient, and that the gestural repertoires of subadults exhibit the greatest variety.

Although recent studies provide evidence that gestures play an important role in the communication of gorillas (*Gorilla gorilla*) [Pika et al., 2003; Tanner & Byrne, 1999], relatively little is known about gestural communication in the third African ape species, the bonobo (*Pan paniscus*) [but see Boesch et al., 2002; Kano, 1992; Susman, 1984; Wrangham et al., 1994]. To date, Nishida and colleagues' [1999] ethogram of the Mahale chimpanzees provides the most complete ethogram of the genus *Pan*. In past publications, researchers of wild populations at Lomako and Wamba, Democratic Republic of Congo, described some gestures (such as *begging*, *branch-dragging*, *drumming*, *embracing*, *presenting*, *rocking*, and *staring*) that are performed in different contexts [e.g., Badrian & Badrian, 1984; Ingmanson, 1996; Kano, 1980; Kuroda, 1980, 1984a]. For captive bonobos, Savage-Rumbaugh and colleagues [Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977] cited 20 gestures that are used in the sexual context. In addition, de Waal [1988] provided a comparison of the communicative repertoires of bonobos and chimpanzees that described 15 distinct gestures of bonobos linked to particular situations. The majority of these gestures are imperative, which means that they are used to get another individual to help in attaining a goal [cf., Bates, 1976]. Declarative gestures, on the other hand, are used to draw another's attention to an object or entity merely for the sake of sharing attention (e.g., holding up an object and showing it [Bates, 1976]). However, referential gestures, such as imperative pointing or declarative gestures, have been reported for only one individual in the wild [Vea & Sabater-Pi, 1998] and human-raised bonobos [Savage-Rumbaugh et al., 1986]. Interestingly, Savage-Rumbaugh and colleagues [Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977] reported some gestures that they consider iconic (depict motion in space) uses of gestures.

These gestures were performed by a bonobo male moving his hand across a female's body, indicating the action he wanted her to perform, or the position he wanted her to take. Roth [1995] tried to support these findings with a follow-up study on 20 bonobos from three different groups, but found no evidence for either the iconic use of gestures or gestures that were correlated with positioning or utilized to negotiate a copulatory position. According to Roth [1995], gestures during sexual encounters only determine whether a sexual interaction will take place.

However, all of the above-mentioned studies lack a clear definition of the term ''gesture,'' and none investigated the flexibility of gestures [e.g., Bruner, 1981; Tomasello et al., 1989]. Flexibility of gestural use, however, may indicate underlying complex cognitive processes, and provides insight into the question as to whether signalers and recipients understand the way the signals function. In addition, none of the aforementioned studies provided an inventory of bonobo gestures and a systematic comparison between studies.

The aim of this study, therefore, was to provide such information based on the following definition [Pika et al., 2003]: A gesture is an expressive movement of limbs or head and body postures that appears to transfer a communicative message, e.g., a request and/or a desired action/event (e.g., play, nurse, or ride) and is accompanied by the following criteria: gazing at the recipient and/or waiting until after the signal has been produced [e.g., Bruner, 1981; Tomasello et al., 1989]. Therefore, gestures that appear to have components of ritualized morphology (e.g., present) are included in this definition only if they meet the criteria outlined above.

We set out with three major goals. The first goal was to enhance our knowledge and understanding of gestural communication in bonobos by compiling a gestural inventory, and to create a baseline of general termini of gestures. This inventory is based on observations of seven subadult bonobos from two family groups, and all substantial descriptions of gestural signals and similar behaviors that have been recorded for bonobos in wild and captive groups. We focused especially on the gestural signaling of subadult bonobos to enhance findings on the communicatory signaling of subadult chimpanzees [e.g., Tomasello et al., 1994] and subadult gorillas (*Gorilla gorilla*) [Pika et al., 2003], to enable a comparison of all African ape species.

Our second goal was to investigate the learning of gestures by focusing on individual and group variability to distinguish between underlying social and individual learning processes.

The third goal concerned the use of gestures, and consisted of three parts: First, we investigated the response of the recipient toward a gestural signal, to make inferences about the role of gestures in the communication of bonobos. Second, we examined how flexibly the gestures were used–for instance, whether the same signal was performed in different contexts, and whether several signals were used within the same context (following Tomasello et al. [1994]). Third, we sought to determine whether bonobos accommodate their use of gestures to the attentional state of the recipient–for example, by using visual gestures only when the recipient is looking.

MATERIALS AND METHODS

Subjects

Seven subadult bonobos, captive-born and naturally raised, were observed at Zoo Apenheul, Apeldoorn, The Netherlands, and the Wild Animal Park

TABLE I. Individuals, Names, Age, Sex, and Location

Name	Age	Sex	Zoo
Unga	8.5 years	Female	Planckendael
Vifijo	6 years	Male	Planckendael
Zomi	3.6 years	Female	Planckendael
Liboso	3.5 years	Female	Apenheul
Zamba	3.3 years	Male	Planckendael
Tarishi	2.8 years	Male	Apenheul
Kumbuka	1.10 years	Female	Apenheul

Planckendael, Plackendael, Belgium. The subadult subjects of this study, and their age, sex, and location at the time of this study are listed in Table I.

Zoo Apenheul, Apeldoorn, The Netherlands

The subjects were three infant bonobos (0–48 months old; the age classes are similar to those established by Thompson-Handler and colleagues [1995]). In addition, the group contained three adult males and five adult females. During the day, the bonobos had permanent access (except during cleaning hours in the morning) to a seminatural island (4,670 m^2) made up of trees, tree trunks, bushes, a wooden climbing facility, and a water ditch, and indoor facilities (750 m^3) that contained ropes and metal climbing bars.

Wild Animal Park Planckendael, Plackendael, Belgium

The subjects were two infants, one juvenile (48–84 months old), and one adolescent bonobo (84–132 months old). In addition to the four subadult bonobos, the group consisted of two adult males and four adult females. During the day, the bonobos had permanent access (except during cleaning hours in the morning) to an indoor enclosure (600 m^3) and an outdoor seminatural compound ($\approx$ 3,000 m^3). The enclosures contained ropes, metal climbing bars, and toys.

Both groups were fed five to six times a day with a wide variety of fruits, vegetables, stems, leaves, and wood, supplemented by primate pellets, vitamins, mineral drinks, and mash. Water was freely available throughout the day.

Observational Procedure

Data were collected May–September 2001 by one observer in the public areas. The two groups were observed 4–7 hr per day. To establish a complete gestural inventory of all subadult bonobos, each focal animal was observed 20 hr (for a total of 140 hr) by means of focal animal sampling (sampling rule: focal animal sampling; recording rule: continuous recording [Martin & Bateson, 1994]). Subsequently, the communicative behavior of each focal animal was videotaped for a total of 15 hr per individual using a digital camera (Sony DCR-TRV900E) and behavior sampling (sampling rule: behavior sampling; recording rule: continuous recording). These techniques resulted in a total of 235 hr of observation and 33 hr of videotape (MiniDV, Sony) of bonobo interactions.

Coding Procedure

We coded the videotapes using a video walkman (Sony, MiniDV, GV-DV-D900EPAL) with a slow-playback function and the coding program Interact 6518.

We only coded those gestures that included gazing at the recipient, gaze alternation, and/or response waiting. Gestures during play bouts or other interactions were coded only when the interaction had stopped for more than 5 sec.

The following variables were coded for each signal:

1. Actor: Sender of the signal.
2. Recipient: Receiver of the signal.
3. Gesture: Table III provides a gestural inventory in which gestures are divided into three signal categories: auditory, tactile, and visual (see definition below).
4. Iconic gesture: According to Tanner and Byrne [1996], the term ''iconic'' refers to a gesture that depicts motion in space or the form of an action.
5. Context: a) Affiliative: grooming, body contact, or protection; b) agonistic: aggressive and submissive behaviors, such as avoiding, crouching, chasing, biting, hitting, or threatening; c) food: intake of food and water; d) nurse: behaviors such as request for nurse, drinking; e) play: includes play-wrestle, play chase, and rough-and-tumble play; f) ride: sit on another individual's back or attempt to do so; g) travel: behaviors including moving around in the enclosure, leaving, and arriving; h) sex: behaviors such as mounting, inspecting genitals, and genital-genital rubbing (GG-rubbing); and i) other: behaviors that occurred infrequently (less than twice) while gestures were used, such as appeasement, exploration, support, and solitary play.
6. Attentional state of recipient: a) direct eye contact or head directed toward the actor, b) head turned 90° away from the actor, and c) head turned more than 90° away from the actor.
7. Response: a) no reaction, b) attentional state of recipient changes (not looking–looking), c) recipient uses a gesture, and d) interaction follows (grouped in the most frequent functional categories; see Context).

Reliability

Ten percent of the videotapes were coded for accuracy by a second observer. A reliability test to measure the agreement of two independent observers was done with the use of Cohen's Kappa, the coefficient of which is defined on a square $r \times r$ contingency table, correcting for the possibility of chance agreement. Cohen's Kappa for the agreement of the definition of gestures was 0.72, which is an ''excellent'' level of agreement [Fleiss, 1981].

Data Analysis and Statistics

Gestural inventory

Only gestures that were observed two times in at least two individuals [Tomasello et al., 1985] were included in the further analysis. Idiosyncratic gestures, which are exclusive to single individuals only, had been observed at least three times. To ensure that the observation period was long enough for all individuals, we plotted the cumulative numbers of observed behaviors vs. time. If an asymptote was reached and no further new gesture was seen for at least 4 days, we concluded that we had observed the individual's current repertoire. However, very rare behaviors, such as gestures that occur only during certain stages in life (e.g., adolescence or estrus), may not have been detected by this design.

To create a baseline of general termini of gestures, we adopted the ''verb first'' principle (putting verbs in front of nouns or adjectives to describe behavioral patterns) introduced by Nishida and colleagues [1999]. Therefore, gestural movements are provided in the form of verbs (e.g., *grab* and *kick*). In

addition, anatomical elements or locations (such as *grab penis* or *slap ground*) were added if they were sufficient or necessary for the differentiation of similar terms (e.g., *slap* and *slap ground*). We adopted as many terms as possible from previous studies–particularly Tomasello and colleagues [1985, 1989, 1994], Pika and colleagues [2003], Savage-Rumbaugh and colleagues [Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977], and de Waal [1988, 1989] to enable within- and between-species comparisons. Descriptions of gestures (see Table III) and similar behaviors from other studies are listed separately and, due to different observational criteria, in their original form. The possible functions of the gestures derive from a quantitative contextual analysis of the response of the recipient toward a gesture in the form of an interaction.

Based on auditory, tactile, and visual components, we formed three signal categories: 1) auditory gestures that generate mainly sound while performed, 2) tactile gestures that include physical contact with the recipient, and 3) visual gestures that generate a mainly visual component with no physical contact.

Group differences

High levels of concordance of gestural repertoires within a group and group-specific gestures would provide evidence for the existence of a social learning process, whereas individual differences that overshadow group differences (i.e., a lack of systematic group differences, and idiosyncratic gestures) imply that mainly an individual learning process is involved. To assess the degree of concordance in the performance of gestures between and within the two groups, we used Cohen's Kappa statistics, with an individual either agreeing or disagreeing on the performance of each gesture as compared with each other individual [c.f., Tomasello et al., 1997]. We calculated two sets of Kappa values for each individual: average concordance with members of the individual's own group, and average concordance with members of the other group. To calculate the values for each individual, we used a matrix method whereby each individual received an average score for its agreement with each other individual based on a comparison of all performed gestures. We then averaged these scores across individuals to obtain group variables.

Adjustment to audience effects

To determine whether bonobos adjust their use of gestures to the attentional state of the recipient, for every gesture the state of the recipient was coded (see Coding Procedure) and then correlated with the signal class of gesture involved (e.g., auditory).

Mean values in the text are reported $\pm$ the standard deviation (SD).

RESULTS

Gestural Repertoire and Inventory

By plotting the cumulative numbers of observed gestures by individual and times for all bonobos, an asymptote of gestures was reached. We concluded that we had observed the current repertoires of all seven individuals. Overall, we observed a total of 1290 signals, which could be divided into 20 different distinct gestures (see Table II, performance of gestures). They consisted of one auditory (5%), eight tactile (40%), and 11 visual (55%) gestures. These gestures were performed mainly in the play context (55%), but also in the food (14%), travel (10%), nurse (5%), ride (5%), sex (5%), affiliative (3%), and agonistic (3%)

TABLE II. Performance of Gestures*

	Unga	Vifijo	Liboso	Zomi	Zamba	Tarishi	Kumbuka	%
Grab	×	×	×	×	×	×	×	100 (N=7)
Slap	×	×	×	×	×	×	×	100 (N=7)
Touch	×	×	×	×	×	×	×	100 (N=7)
Peer		×	×	×	×	×	×	86 (N=6)
Jump		×	×	×	×		×	71 (N=5)
Move	×		×		×	×	×	71 (N=5)
Push		×	×	×		×	×	71 (N=5)
Gallop		×		×		×	×	57 (N=4)
Reach arm				×	×	×	×	57 (N=4)
Kick				×	×	×	×	57 (N=4)
Ice skating		×			×	×		43 (N=3)
Somersault		×		×	×			43 (N=3)
Look at						×	×	43 (N=3)
Punch	×	×			×			43 (N=3)
Shake	×				×			29 (N=2)
Stomp					×	×		29 (N=2)
Bob		×			×			29 (N=2)
Pull		×			×			29 (N=2)
Grab-pull-push	×				×			29 (N=2)
Present			×		×			29 (N=2)

*Percentage for all individuals.

contexts. In addition, we observed three idiosyncratic gestures that were performed by three different individuals: Zamba from the Planckendael group performed the gesture *slap ground*, Tarishi from the Apenheul group performed *swagger quadrupedal*, and Kumbuka (also from the Apenheul group) performed *grab penis*.

The tactile gestures *grab*, *slap*, and *touch* were performed by all seven individuals, whereas the performance of the other 17 gestures showed a high degree of variability (see Table II). On average, each individual used 11 (± 2.8) gestures.

We did not observe any instances of iconic use of gestures.

In Table III we compiled a gestural inventory of bonobos based on the results of the present study and descriptions of gestures or similar behaviors from other publications of wild and captive groups. Based on a quantitative contextual analysis of the response of the recipient (in form of an interaction), we analyzed the function of each gestural signal, as listed below.

Learning

To investigate whether group-specific differences could be found, we performed two sets of analyses, reported in the two subsections below. First, we investigated the concordance between and within groups. The second analysis examined whether we could detect group-specific gestures that could not be explained by environmental differences or social settings.

Concordance between and within groups

To assess the degree of concordance in the performance of gestures between and within the two groups, we used Cohen's Kappa statistics (see (Data analysis and statistics)). The between (mean=0.45 ± 0.13) and within-group (Apenheul

TABLE III. Gestural Inventory and Function*

THIS STUDY	Other captive studies	Studies in the wild
	Same gestures or similar behaviors named with different terms	Same gestures or similar behaviors named with different terms
Auditory gestures	**Auditory gestures**	**Auditory gestures**
	Chest beat: Animal slaps repetitively on own chest with alternating open hands or knuckles (2).	
(**Clap**: Palms of hands, two feet, or a hand and a foot contact in space in front of body: was only observed towards visitors.)	**Clap**: Palms of hands, two feet, or a hand and a foot contact in space in front of body (2,7).	**Clap**: (11).
		Leaf clip: Ripping of leaves from ground vegetation or from trees (13).
		Leaf clip by mouth: Animal rips leaves from herbs or trees and holds them in her mouth (13).
		Leaf strip: Animal tears leaves from saplings or branches (13).
Slap ground: Animal hits/drums ground with the palm of one or both hands (idiosyncratic gesture). Response: Play 83.3%; affiliative: 16.6%.	**Rhythmic movements**: A series of rhythmic slapping movements with the hands or **Stomping** with the feet on the ground (2); **Stomp** (4) or **Drum on an object** (4).	**Branch slap**: While sitting in a tree, animal slaps noisily on either the branch supporting her or the tree's trunk (13).
Stomp: Animal brings the sole or heel of foot suddenly and forcibly against or upon the ground, object, or walks in a pounding manner. Response: Travel: 100%.		**Buttress beat**: Animal runs up buttress roots of large trees and slap/stamp on them with their hands and feet (13).
		Drum: Hit and/or kick tree trunks especially those with buttresses (8); At Wamba animals **drum** with their feet (7); At Lomako animals drum with hands alone or with hands and feet (13).
		Stomp: Only against humans (6). **Stamp**: While running not while sitting→**Stamping run** (8).
Tactile gestures	**Tactile gestures**	**Tactile gestures**
	Embrace: Arm of sender is stretched and raised till about head level with the palm facing downward or placed lightly on the recipient's body (1).	**Embrace**: (6).
		Embrace half: Animal puts one arm around another as in a half embrace (11).

Lateral embrace: Gently placing one arm around the other's shoulder, back, or waist, or putting both arms around the other while pulling the recipient closer (2).
Ventral embrace: Both arms are opened and the partner is hugged ventro-ventrally, with bellies touching (2).

Grab: Position partner's lower body with both hands (3).

Grab (8,11)

Hunch over: One arm or entire body is moved over or briefly pressed on the crouching partner. The main difference with the lateral embrace is the absence of hugging, and the position of the actor above the recipient (2).

Hunch quadrupedal: See visual gestures

Kick: (9)

Kick: (6,8,11).

Mouth kiss: The open mouth is placed over the partner's mouth. Extensive tongue–tongue interaction (**Tongue kissing**) was observed in a quarter of the instances (2), mouth kiss (4).

Mock bite: Keep mouth wide open without the retraction of lips and press the teeth to the back, shoulder or other body part without biting (8).

Kiss with open-mouth Is directed only to infants and juveniles by older bonobos and never seen between adults (8).

Move hand and arm across body: (3).
Move hand toward another portion of cage: (3).

Grab: Animal grasps another animal with the whole hand, fingers are bent. Response: Play: 41.5%; agonistic: 30.8%; travel: 23.2%; affiliative: 1.5%; ride: 1.5%; other: 1.5%.
Special form:**Grab Penis** (idiosyncratic).
Grab-push-pull: Movement series which includes the animal grabbing another animal and directly pulling or pushing it. Response: Agonistic: 50%; nurse: 16.7%; ride: 16.7%; other: 16.6%.

Kick: Animal uses legs to forcefully move another animal away. Response: Play: 54.5%; agonistic: 27%; travel: 9%; other: 9%.

TABLE III. Continued

	Pat: One hand is placed on the partner's body, usually the head or back, and a series of gentle patting or stroking movements is made (2,4).	**Pat:** Shown only by juvenile bonobos (8).
Pull: Animal grasps another animal and forcefully moves her closer. Response: Play: 50%; sex: 25%; other: 25%.	**Pull: Pull toward self by putting arm around partner's back** (3);**Pull limb toward self** (3);**Over:** Individual placing a hand on the shoulder or back of the recipient and pulling that subject with the hand in a sideway motion (1).	**Pull:** (8,11).
Punch: Animal performs a brief forward or downward thrust on or against another animal with fist/knuckles or finger. Response: Play: 50%; travel: 25%; agonistic: 25%.	**Punch:** 2 out of 10 individuals (2).	**Poke:** Prodding repeatedly with fingertip contact with one or two extended fingers to an infant's ventrum while lying on its back (11).
Push: Animal uses arms or legs to forcefully move another animal away. Response: Travel: 53.8%; play: 30.8%; food: 7.7%; agonistic: 7.7%.	**Push:** Differentiation between **Push limb across body** (3); **Push leg or arm out from body** (3); **Push under chin** (3). **Rest knuckles on arm or back:** Sender is placing a hand on shoulder or back of recipient (3).	**Push:** (11).
Slap: Animal hits another animal forcefully with the palm of the hand. Response: Play: 50%; travel: 19.2%; agonistic: 15.4%; sex: 7.7%; other: 15.4%.	**Slap:** Male uses the back of an outstretched hand to hit the inside of the females legs so that she opens them (1).	**Slap/Hit:** (8). **Groom slap:** A groomer may suddenly strike the groomee with a flat palm, making a sound that is audible to human observers up to about 20 m away. A slap might coincide with a change of grooming position (13).
Touch: Gentle and short (<5 sec) contact with flat hands, body part, or feet. Response: Play: 28.5%; travel: 28.5%; agonistic: 10.7%; other: 7.1%; ride: 10.7%; sex: 7.1%; affiliative: 3.6%; nurse: 3.6%.	**Touch: Touch outside of partner's shoulder hip or thigh and motion across body with hand and forearm movement** (3);**Touch hand or arm and motion outward from partner's body** (3);**Touch shoulder or back and move hand toward self** (3);**Touch head, chin, or inside of shoulder and lift hand upward** (3);**Touch partner and walk to other end of cage** (3);**Rest knuckles on arm or back and move arm toward self** (3);**Move hand and forearm across body** (3).	**Touch:** (6,11).

Visual gestures

Visual gestures

Visual gestures

Bow: Animal raises and lowers its torso by stretching and flexing the limbs alternating includes also movements such as nod head, shake head, tip head or turn head. Response: Play: 58.3%; travel: 16.6%.

Gallop: Animal runs very fast toward or close to another animal. Response: Play: 44.5%; agonistic: 33.3%; travel: 22.2%.

Ice skate: Animal pirouettes with hands on the ground or in the air. Response: Play: 100%.

Jump: Animal springs from or over an object close to another animal or on an animal. Response: Play: 62.5%; travel: 25%; agonistic: 12.5%.

Arm up: One half bended arm is lifted, opening a sitting place at the performer's side. A lateral embrace results when the partner accepts the offered place (2).

Bipedal stand: Animal stands on both legs in an upright posture or **Raise body up and back up while standing bipedal**(3). **Head shake**:(4). **Body shake, raise head back, sway; Shake head horizontally or circularly** (3).

Jump-stamp: (3)

Aimed throw: Animal throws sticks and branches at human observers and at conspecifics (13).

Bow: Absent in bonobos (11). Other description might be **rocking**, vary from slight to intense swaying; Differentiation between **Squatting, Bipedal** and **Quadrupedal rocking**, could include arm raising(6); movement of the squatting body up and down, forward and backward or side to side (8). **Tip head**: (8).

Crouch: Quadrupedal posture with limbs flexed, hindquarters not turned towards another animal (8).

Groom-hand-clasp: One animal raises the arm of another animal to access the underarm (8). **Hand clasp**: Hand clasping by Lomako bonobos differs in that, a) the two individuals do not simultaneously groom, and b) the hand clasp results from the action of only one individual (13).

Hunch quadrupedal: Stand, walk, or run on all fours with rounded back and head pulled in between shoulders (11).

Pirouette: Probably absent in the bonobos of Wamba (8).

TABLE III. *Continued*

Look: Gaze at partner in a very direct manner. Response: Travel: 37.5%; ride: 25%; affiliative: 12.5%; sex: 12.%; other: 12.5%.	**Look at**: Walk on other end of cage and gaze at partner (3).	**Look**:(10); **Look back**: Animal looks back at another individual in order to monitor the following or grooming individual (11).
		Lower: **Lower arm**: Grooming animals lowers arm (11). **Lower head**: Two animals face each other in social grooming, and one partner flexes the neck to offer the top of head for grooming (11). **Lower leg**: Resting or lying animals lowers raised leg.
Move: Animal moves an object in front of another animal, for instance a branch, straw etc. Response: Affiliative: 40%; play: 30%; agonistic: 20%; sex: 10%.		Seewave
Peer: Animal sits or stands very close and puts her lips/face very close to the lips/face or hand of a feeding partner. Another form is begging with a hand, which is outstretched with palm facing up toward another animal. Response: Food: 28.6%; travel: 28.6%; agonistic: 14.3%; play: 14.3%; other: 14.2%.	**Peer/Beg**: (3; 4; 5); **Hand-up begging** (2); **Hand-side begging** (2); **Leg-out begging** (2); **Flexing**: The hand is stretched out to the other in the same manner as in the begging gesture, but with a rapid alternation of stretching and bending movements of the four fingers (2).	**Peer**: (8,10,12); **Holding out the hand**: (8); **Extended hand, palm upward/beg**: (8,14); Staring: (6); Beg (8).
Present: Animal presents genital region ventrally, rump or belly or penis. Response: Affiliative: 60%; sex: 20%; other: 20%.	**Present**: Differentiation between concave back, ventrally present and rump present (2); present penis (4).	**Present**: (6,11).
Reach: Animal stretches out a limb towards another animal. Palm facing sideways or downward. **Response**: Travel: 50%; play: 30%; agonistic: 10%; affiliative: 10%.	**Raise arm**: (3); **Raise arm and flip** (3); **Out**: (1); **Move hand toward another portion of cage**: (3). **Raise up**: Stand bipedal; arm is partially extended across and flipped upward (3).	**Raise**: Elevate limb while lying supine or sitting on the ground (11). **Reach**: (6); **Extend hand, palm downward**: (11).**Extend leg**: Reach leg instead of hand to another individual (11).
Shake: Animal hangs upside down from a branch or rope and moves legs/arms from side to side in front of another animal. Response: Play: 66.6%; agonistic: 33.3%.		**Upside-down suspension**: (8).

Somersault: Animal makes a flip. Response: Play: 83.3%; affiliative: 16.6%.

Stretch over: The arm is stretched and raised until about head level with the palm facing downward (2).

Swagger quadrupedal: Animal sways back and forth quadrupedally (idiosyncratic). Response: Nurse: 50%; travel: 50%.

Swagger: In an upright or semi-upright posture an animal sways, often rhythmically, from one foot to the other. The animal may remain in one spot to swagger or more forward during the swagger. The arms are normally held out from the body, the shoulders hunched up (8). **Swaying back:** (12).

Wave: The stretched arm is brought high up in the air, above the head, with the hand palm facing the partner (2). Stand bipedal and wave arms out from body (3).

Wave: Wave using a branch (only against humans) (6), (7). **Drag branch:** A branch broken from a tree, or one lying on the ground is dragged by one hand during a charging display (8,11,13,14). **Branch flailing** appears as an element of it (8). **Branch-shake:** A branch is shaken with quick jerky movements of the arm, slight or vigorous, while the animal is sitting or standing (8). Directed at humans, monkeys, or conspecifics (13).

Wrist shake: The arm(s) and hand(s) are stretched out to the other while vigorously shaking the wrist, resulting in lateral flapping movements of the hand; seen in 3 out of 10 individuals (2), (3), (5); circle: (1).

*Description and signal categories of gestures and functions in this study, and descriptions and signal categories of gestures in other studies: 1, described by Roth [1995]; 2, described by de Waal [1988]; 3, described by Savage & Bakeman [1978] and Savage-Rumbaugh et al. [1977]; 4, described by Patterson [1979]; 5, described by Vineberg [1977]; 6, described by Kuroda [1984a, b, 1980]; 7, described by Ingmanson [1987]; 8, described by Kano [1992, 1998]; 9, described by Tratz & Heck [1954]; 10, described by Idani [1991, 1995]; 11, described by Nishida et al. [1999]; 12, described by Furuichi [1989]; 13, described by Hohmann & Fruth [2003a, b]; 14, described by Badrian & Badrian [1984].

group: mean=0.46±0.2; Planckendael group: mean=0.55±0.18) Kappas showed very low degrees of concordance [Altmann, 1991] and were highly similar. Although the within-group Kappas were slightly higher than the between-group Kappas, an analysis of the individual Kappas of average concordance with group members and with members of the other group did not show a significant difference (Wilcoxon-test: Z=−0.845, P=0.398, n=6).

Group-specific gestures

We found group-specific differences in the performance of two distinct gestures. The gesture *punch* was exclusive to bonobos in the Apenheul group, whereas the gesture *somersault* was performed only in the Planckendael group. *Punch* was performed by all three subadults, and *somersault* was performed by three of four individuals.

Use

Response

To investigate the use of gestures, we focused on the response of the recipient toward a gestural signal (see Fig. 1a). On average, 23.5% (±8.93%) of the gestures did not receive a response, 13.5% (±3.15%) led to a change in the attentional state of the recipient (not attending changed to attending), 15.5% (±4.62%) received a response in form of a gesture, and 40% (±11.94%) led to an interaction between the signaler and the recipient. These interactions could be grouped in the following contextual categories (see Fig. 1b): overall play: 40%; travel: 24%; agonistic: 14%; affiliative: 6.5%; other: 5%; sex: 4%; nurse: 3%; ride: 2%; and food: 1.5%. In such cases in which a gesture did not receive a response, the signaler used in 30% a second gesture.

One signal in several contexts

To investigate the flexibility of gestural signals, we analyzed whether they were used in different contexts, whether several signals were used within the same context, and/or whether gestures were adjusted to the attentional state of the recipient.

The diagram in Fig. 2a demonstrates that with respect to the number of all performed gestures, 10 of 20 gestures (50%) were performed in only one context, and 50% were observed in more than one context. Seven gestures (35%) were performed in two contexts, two gestures (10%) were observed in three contexts, and one gesture (5%) was performed in five contexts. Tactile gestures occurred more frequently in two contexts (mean of 2.13 contexts/individual, ±1.36; see Fig. 2b) than visual gestures (mean of 1.55 contexts/individual, ±0.69), but the differences were not significant (MWU TAC>/<VIS: Z=−9.431, two-tailed, P=0.395, n_{Tac}=8; n_{vis}=11). Overall, each individual used on average 2.7 (±1.48) gestures in more than one context.

One context with several signals

The results indicate that in every context on average approximately two (±0.6) different gestures were used. Figure 2c shows that overall in the play context, 19 different gestures (95%) were observed, whereas in the agonistic and affiliative contexts only 10% of all gestures occurred. In the travel context 25% (five gestures) of all gestures were used. In the food, sex, and ride contexts 20% (four gestures) of all gestures were used, and in the nurse context 15% (three gestures) of all gestures were used. These differences between the occurrence of
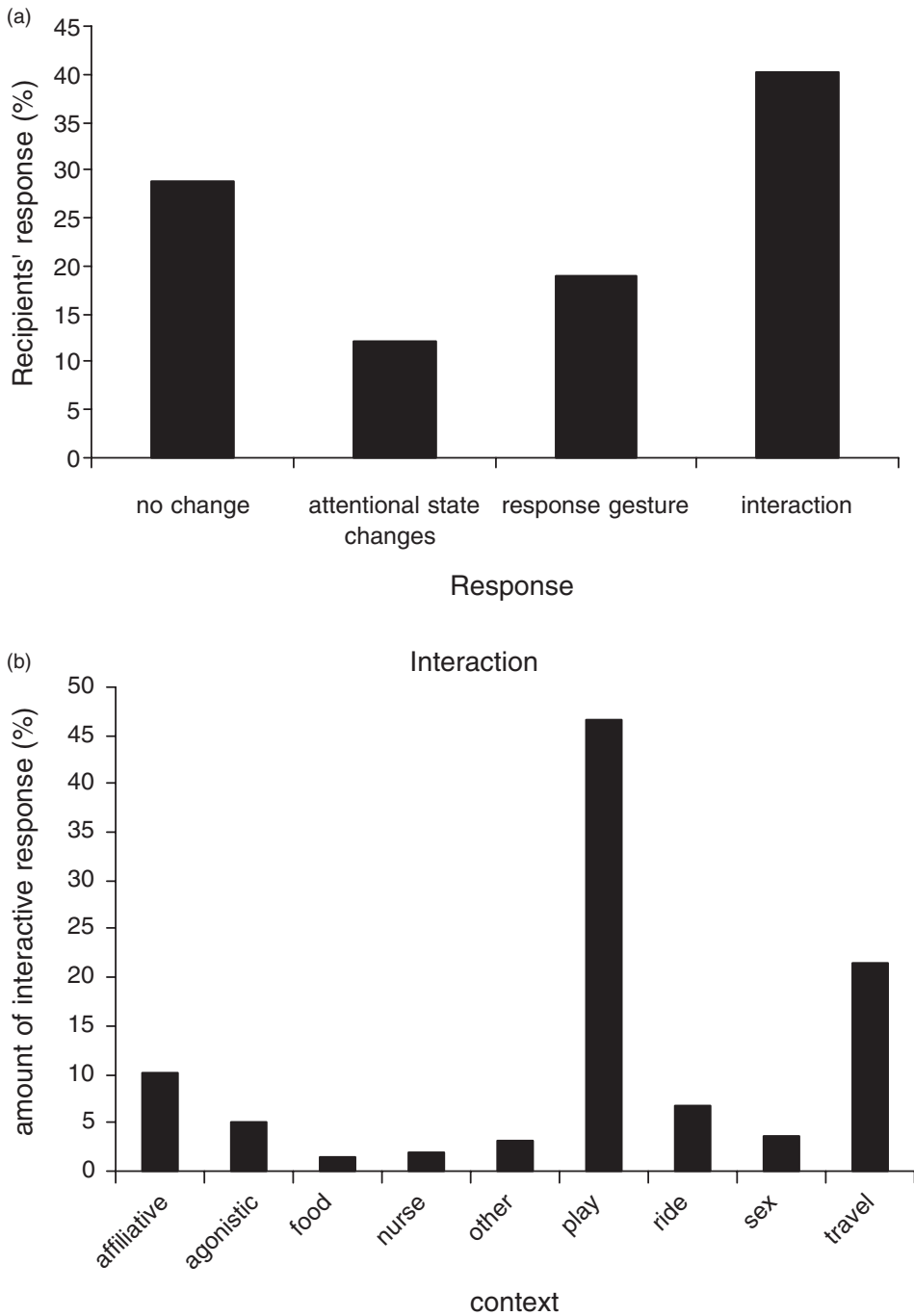
Fig. 1. **a:** Recipient's response per observed gesture, in percent. **b:** Recipient's type of interactive response per interaction, in percent.
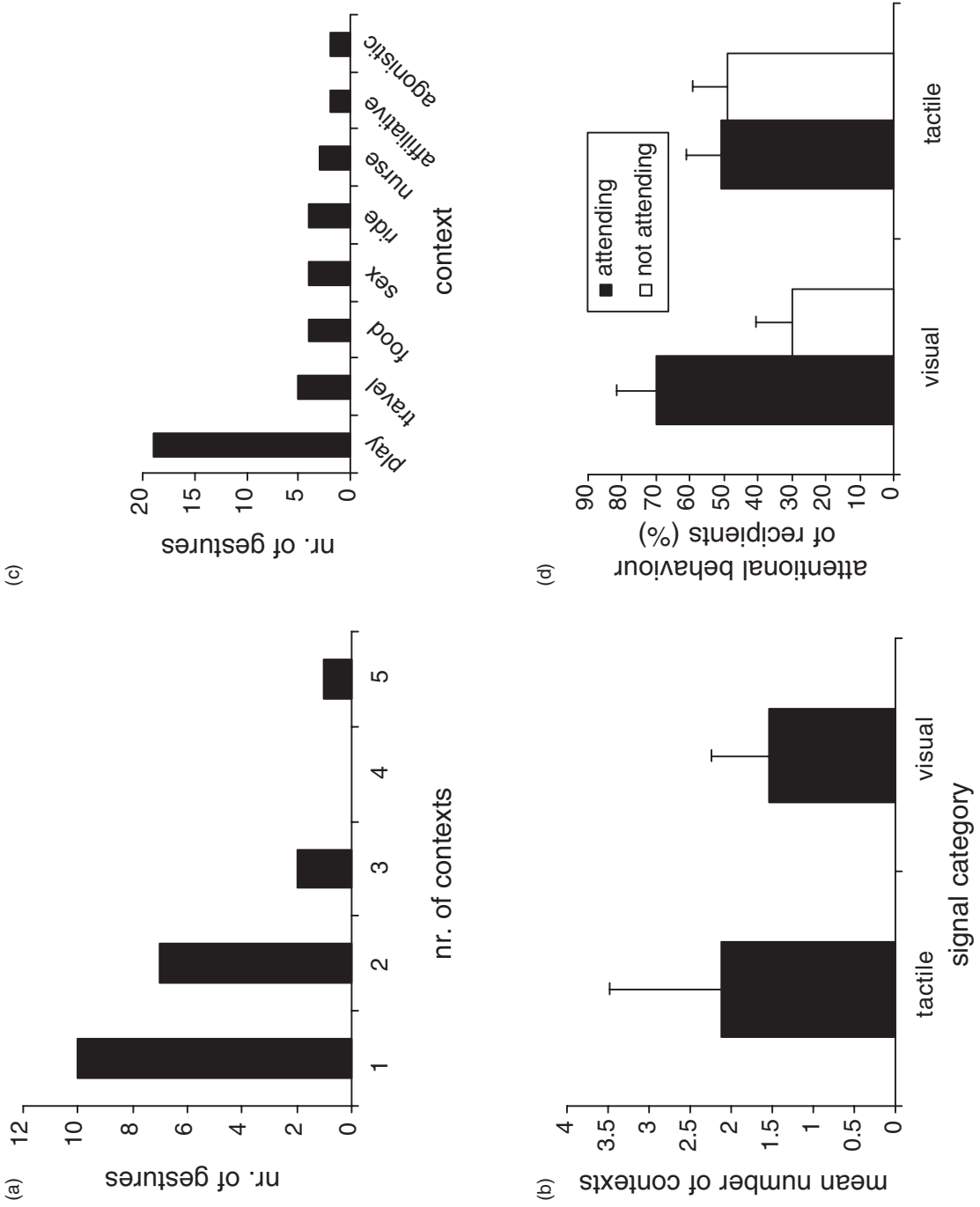
Fig. 2. Flexibility of use: (**a**) number of gestures observed in different contexts, (**b**) mean number of gestures per context, (**c**) number of contexts for tactile and visual gestures, (**d**) adjustment to audience effects. Error bars indicate the SD.

TABLE IV. Wilcoxon Signed Rank Test*

Play vs. food	$Z=-3.873$, $P<0.001$, n=15
Play vs. ride	$Z=-3.873$, $P<0.001$, n=15
Play vs. nurse	$Z=-4.000$, $P<0.001$, n=16
Play vs. travel	$Z=-3.742$, $P<0.001$, n=14
Play vs. affiliative	$Z=-4.123$, $P<0.001$, n=17
Play vs. agonistic	$Z=-4.123$, $P<0.001$, n=17
Play vs. sex	$Z=-3.873$, $P<0.001$, n=15

*Z-values for comparison of different numbers of gestures per context.

signals due to different contexts were significant for the play context vs. all other contexts (Friedman: $\chi_7^2=89.876$, $P=0.001$; for Z-values of the Wilcoxon-test see Table IV).

Attentional state of the recipient

We found a significant difference between the use of tactile and visual gestures among all individuals based on a variation in the degree of visual attention of the recipient (Wilcoxon-test: $Z=-2.366$, $P=0.018$, n=7). On average, $79\%\pm10\%$ of visual gestures were performed when the recipient was looking, whereas only $50\%\pm10\%$ of tactile gestures were performed to an attending recipient (see Fig. 2d).

DISCUSSION

The three main goals of this article were to 1) compile a gestural inventory for bonobos based on the present and previous studies, 2) investigate how bonobos learn, and 3) examine how they use their communicative gestures.

We have described 20 different distinct gestures of auditory, tactile, and visual signals. Concerning auditory gestures, we observed the gestures *slap ground* and *stomp*, which were also described in other studies using different terms [de Waal, 1988; Hohmann & Fruth, 2003a; Kano, 1998]. Kano [1998] mentioned that bonobos at Wamba only *stamp* while running (*stamping run*). Interestingly, in the bonobo group at the San Diego Zoo, de Waal [1988] observed the auditory gesture *chest beat*, which is a species-typical gesture for gorillas [Pika et al., 2003] and has not yet been described for other captive or wild bonobo groups. In addition, Ingmanson [1987] and Nishida et al. [1999] reported the use of the auditory gesture *clap* for wild and captive bonobo groups. In wild bonobos at Lomako, Hohmann and Fruth [2003a] observed *leaf clip by mouth*, *leaf clip by hand*, and *leaf string*.

Concerning tactile gestures, we observed the gestures *grab*, *kick*, *pull*, *punch*, *push*, *slap*, and *touch*, which are listed in other studies with the same or similar terms, or are subclassified to provide further details [Kano, 1998; Kuroda, 1980, 1984a, b; Nishida et al., 1999; Roth, 1995; Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977; Tratz & Heck, 1954]. *Grab-pull-push*, however, is a special version of the gesture *grab*, and is not mentioned in any other publication. We did not observe tactile gestures, such as *embrace* described by Roth [1995] and de Waal [1988]; de Waal's [1988] *hunch over*; Savage-Rumbaugh and colleagues' *mouth kiss* [Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977] (also described by de Waal [1988], similar to Kano's [1998] *kiss with open mouth*), *move hand and arm across body*, and *move hand toward another portion of cage*; Kano's

[1998] *mock bite*; and Patterson's [1979] *pat* (also described by de Waal [1988] and Kano [1998] for juvenile bonobos).

Concerning visual gestures, the gestures *bow*, *jump*, *look*, *peer*, *present*, *reach*, and *shake* are described in other studies with either the same term or subclassifications [de Waal, 1988; Kano, 1998; Kuroda, 1980, 1984a, b; Nishida et al., 1999; Patterson, 1979; Roth, 1995; Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977; Tratz & Heck, 1954].

We did not observe certain gestures, such as *aimed throw*, *arm up*, *branch shake*, *crouch*, *drag branch*, *groom-hand-clasp*, *hunch quadrupedal*, *lower*, *stretch over*, *wave*, and *wrist shake*, that were described in other studies [e.g., de Waal, 1988; Ingmanson, 1996; Kano, 1998; Kuroda, 1980, 1984a, b; Nishida, 1990; Patterson, 1979; Roth, 1995; Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977; Tratz & Heck, 1954]. However, we recorded gestures that were not observed in any other study, such as *gallop*, *ice skate* (termed as *pirouette* [Nishida et al., 1999] and probably absent in the bonobos of Wamba [Kano, 1998]), *move*, and *somersault*.

Some of these differences may be due to the different observation designs used. In some cases (e.g., *clap* and *chest beat* gestures) the differences in comparison with other studies appear to reflect different rearing histories, and demonstrate clear group-specific differences. In addition, Savage-Rumbaugh and colleagues [Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977], and Roth [1995] focused on communicative gesturing between adult bonobos in the sexual context. Our differences with these studies may therefore be explained by age differences, and imply that some gestures obtain a function after the animal reaches maturity.

To investigate whether bonobos acquire their gestures via a social or an individual learning process, we focused on concordances in the gestural repertoires within and between groups, and on idiosyncratic and group-specific gestures. We found three idiosyncratic gestures, and showed that the concordances between and within groups were similar. Taking these results as indicators against a social learning process involved, the present findings are consistent with findings on chimpanzees [Tomasello et al., 1994] and gorillas [Pika et al., 2003]. Furthermore, they extend the theory of Tomasello and Zuberbühler [2002] regarding common chimpanzees, and confirm that the main learning process involved in the acquisition of gestures by bonobos is ontogenetic ritualization.

We observed two group-specific gestures (*somersault* and *punch*) that cannot be easily explained by different physical or social settings. The findings of the present study are therefore consistent with observations on group-specific gestures in wild chimpanzees, such as *leaf clipping* [Nishida, 1980], *grooming hand clasp* [McGrew & Tutin, 1978], or the recently recorded *social scratch* [Nakamura et al., 2000]. In addition, they support the findings of de Waal [1988] and Ingmanson [1987], who observed two group-specific gestures (*clap* and *chest beat*) in the bonobo group at San Diego Zoo in the context of grooming. The gesture *clap* was used between conspecifics and was observed in seven animals from three different groups. Interestingly, this behavior was performed only by animals that were human-raised, implying that the gesture *clap* may have been transmitted from humans to bonobos. In addition, Thompson [1994] showed that this gesture spread from the San Diego group to other zoos by the transfer of San Diego individuals to these zoos (for similar results on common chimpanzees, see de Waal and Seres [1997]), suggesting that a social learning process is involved. In addition, in a captive gorilla group at Apenheul Zoo, Pika et al. [2003] recently

observed the group-specific gesture *armshake*. Although the present data are limited due to the small sample size, these results imply that an underlying social learning process is involved in the acquisition of specific gestures (but see Tomasello and Call [1997] for a different opinion), and therefore add fuel to the ongoing debate concerning population-specific differences and ''culture'' in apes [e.g., Boesch, 2003; Hohmann & Fruth, 2003a; Nakamura et al., 2000; Nishida, 1987; Pika et al., 2003; Sugiyama, 1981].

To make inferences about the role gestures play in the communication of bonobos, we analyzed the responses of the recipients toward a gesture. This approach enabled us to investigate whether bonobos use gestures to achieve a certain goal that is understood by the receiver. The results showed that bonobos respond to the majority of all performed gestures by looking at the signaler, performing a response gesture, or interacting with the signaler. In addition, in one-third of the cases the signaler continued to perform additional gestures if the recipient did not react.

Concerning flexibility of use, we found that the bonobos used about 10 gestures in at least two or more functional categories, and in a single context used an average of two different gestural signals. In addition, the bonobos adjusted their use of gestures to the attentional state of the recipient (i.e., performed a visual gesture more often when the recipient was looking than when he was not). These findings are consistent with studies on chimpanzees [Tomasello et al., 1994, 1997] and gorillas [Pika et al., 2003]. Similarly to findings in gorillas, the present study demonstrated that tactile gestures also represent the most flexible gestures (i.e., show the highest variety of functional categories), whereas auditory and visual gestures were linked to fewer contexts (mainly the play context).

Overall, the data indicate that the gestural repertoire of subadult bonobos can be characterized by flexibility with adjustments to communicative circumstances, such as a nonresponding recipient and the attentional state of the receiver. Furthermore, the results imply that 1) signalers use gestures to achieve a certain goal, show persistence to the goal, and understand the way their signals function; and 2) gestures are received as important means of communication by receivers. These results therefore provide strong evidence that gestures function as important communicative means for bonobos.

In 1977, when systematic investigations of the gestural repertoire of chimpanzees [e.g., Goodall, 1986; Plooij, 1978, 1979; Tomasello et al., 1985] and gorillas [Pika et al., 2003; Tanner, 1998] were still lacking, Savage-Rumbaugh and colleagues [1977] argued that the gestural propensity and capability of the pygmy chimpanzee far exceeded those reported for any other ape. This hypothesis was based primarily on observations of sexual encounters among three captive bonobos, and the finding that the single male seemed to use iconic gestures to demonstrate the desired sexual position. In contrast, we observed no instances of iconic use of gestures, although it is possible that our analysis did not focus in sufficient detail on the receiver's response to detect them. However, the results of the present study support the findings of Roth [1995] and strengthen the hypothesis of Tomasello and Zuberbühler [2002] that some data have been overinterpreted. A role for iconicity in the performance and comprehension of gestures by bonobos and other apes has therefore not yet been properly demonstrated [Tomasello & Call, 1997].

Furthermore, a comparison of gestural variations among all African ape species provides evidence that the gestural signaling of bonobos and chimpanzees shows qualitative differences in the agonistic and sexual contexts (for a direct comparison see de Waal [1988]), and that the gestural propensity and variety of

gorillas [Pika et al., 2003] surpasses that of bonobos. The most intriguing differences among the three species become obvious focusing on 1) gestures in the sexual context, 2) the average number of gestures used, 3) the variety of auditory gestures used, and 4) concordances in the performance of gestures within and between groups, as described below:

Gestures in the sexual context

Bonobos use a wider gestural repertoire to solicit sex, such as *bipedal stand*, *ventral present*, *rump present*, *wave*, or *penis offer* [de Waal, 1988; Patterson, 1979; Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977] compared to chimpanzees and gorillas, which may be due to differences in the sexual behaviors of the three species. Compared to chimpanzees and gorillas, bonobos are more sexually active outside the periovulatory period, and bonobos use sexual behavior more to maintain and regulate social relationships [Kano, 1992].

Average number of gestures used

On average, subadult chimpanzees performed 9.5 different gestures [Tomasello et al., 1997], subadult bonobos performed eight different gestures, and subadult gorillas performed 20 different gestures [Pika et al., 2003]. These differences may be due to the fact that individual distances are higher in gorillas [Klein, 1999] than in bonobos and chimpanzees [Harcourt, 1979; White & Chapman, 1994], and therefore gorillas may announce their presence before approaching more often by using gestural communication.

Variety of auditory gestures used

Subadult bonobos performed one auditory gesture, subadult chimpanzees performed four, and subadult gorillas performed six auditory gestures on a regular basis. One explanation for the small number of auditory gestures used may be that bonobos exhibit lower levels of agonistic behaviors [Kano, 1992; but see also Hohmann & Fruth, 2003b], which play an important part in the displays of adult male chimpanzees and gorillas [Goodall, 1986; Schaller, 1963]. In contrast, adult bonobo males mainly use visual gestures such as *bow*, *wave*, and *swagger* in their display behavior [de Waal, 1988; Kano, 1992, 1998; Patterson, 1979].

Concordance in the performance of gestures within and between groups

The gestural repertoires of bonobos (this study) and chimpanzees are characterized by a high degree of variability within and between groups [Tomasello et al., 1997]. In contrast, gorillas show high degrees of concordance both within and between groups [Pika et al., 2003]. These results suggest that the gestural repertoires of the genus *Pan* may be more flexible than those of gorillas.

Based on this qualitative comparison, we hypothesize that the differences in gestural signaling among the three species indicate general communication differences. These have been developed in adaptation to 1) different ecological factors, such as diets and locomotor profiles [Ankel-Simons, 2000; Boesch et al., 2002; Malenky et al., 1994; Robbins, 2001; Taylor & Goldsmith, 2003], and/or 2) different social factors, such as levels of agonistic behaviors [Boesch et al., 2002; Doran & McNeilage, 2001; Furuichi, 1997] and species-typical distances. Our findings may therefore strengthen the hypothesis of Marler [1965] (but see also Maestripieri [1999]), which suggests that an evolutionary trend apparent in primate communication is the preponderance of vocal signals in arboreal species

vs. gestural signals in terrestrial species. This hypothesis implies that the use of gestural signals may be more efficient for the primarily terrestrial gorillas than for the more arboreal bonobos and chimpanzees.

ACKNOWLEDGMENTS

REFERENCES

Altmann D. 1991. Practical statistics for medical research. CRC: Chapman and Hall.

Ankel-Simons F. 2000. Primate anatomy, an introduction. San Diego: Academic Press.

Badrian A, Badrian N. 1984. Social organization of *Pan paniscus* in the Lomako Forest, Zaire. In: Susman RL, editor. The pygmy chimpanzee: evolutionary biology and behavior. New York: Plenum Press. p 325–346.

Bates E. 1976. Language and context: the acquisition of pragmatics. New York: Academic Press. 616 p.

Boesch, C. 1995. Innovation in wild chimpanzees. Anim Behavior 48:653–667.

Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Tai Forest. Oxford: Oxford University Press. 316 p.

Boesch C, Hohmann G, Marchant LF. 2002. Behavioral diversity in chimpanzees and bonobos. Cambridge: Cambridge University Press. 296 p.

Boesch C. 2003. Is culture a golden barrier between humans and chimpanzees? Evol Anthropol 12:82–91.

Bruner J. 1981. Intention in the structure of action and interaction. In: Lipsitt L, editor. Advances in infancy research. Norwood, NJ: Ablex. p 41–56.

Call J. 1999. Levels of imitation and cognitive mechanisms in orangutans. In: Miles HL, editor. The mentalities of gorillas and orangutans. Cambridge, UK: Cambridge University Press. p 316–341.

de Waal FBM. 1988. The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. Behaviour 106:183–251.

de Waal FBM. 1989. Behavioral contrasts between bonobo and chimpanzee. In: Marquardt LA, editor. Understanding chimpanzees. Cambridge, MA/London, England: Harvard University Press w/ Chicago Academy of Sciences. p 154–175.

de Waal FBM, Seres M. 1997. Propagation of handclasp grooming among captive chimpanzees. Am J Primatol 43:339–346.

Doran DM, McNeilage A. 2001. Subspecific variation in gorilla behavior: the influence of ecological and social factors. In: Stewart KJ, editor. Mountain gorillas: three decades of research at Karisoke. Cambridge: Cambridge University Press. p 123–149.

Fleiss J. 1981. Statistical methods for rates and proportions. New York: John Wiley & Sons. 800 p.

Furuichi T. 1989. Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. Int J Primatol 10:173–197.

Furuichi T. 1997. Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. Int J Primatol 18:855–875.

Goodall J. 1986. The chimpanzees of Gombe, patterns of behaviour. Goodall J, editor. Cambridge, England: Belknap Press of Harvard University Press. 673 p.

Harcourt AH. 1979. Social relationships between adult male and female mountain gorillas in the wild. Anim Behav 27:325–342.

Heyes CM. 1994. Social learning in animals: categories and mechanisms. Biol Rev Cambr Phil Soc 69:207–231.

Hohmann G, Fruth B. 2003a. Culture in bonobos? Between-species and with-species variation in behavior. Curr Anthropol 44:563–571.

Hohmann G, Fruth B. 2003b. Intra- and intersexual aggression by bonobos in the context of mating. Behaviour 140:1389–1413.

Idani G. 1991. Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. Folia Primatol 57:83–95.

Idani G. 1995. Function of peering behavior among bonobos (*Pan paniscus*) at Wamba, Zaire. Primates 36:377–383.

Ingmanson EJ. 1987. Clapping behavior: nonverbal communication during grooming in a group of captive pygmy chimpanzees. Am J Phys Anthropol 72:214.

Ingmanson EJ. 1996. Tool-using behavior in wild *Pan paniscus*: social and ecological considerations. In: Parker ST, editor. Reaching into thought: the minds of the great apes. Cambridge: Cambridge University Press. p 190–210.

Kano T. 1980. Social behaviour of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: a preliminary report. J Hum Evol 9:243–260.

Kano T. 1992. The last ape: pygmy chimpanzee behavior and ecology. Stanford, CA: Stanford University Press. 248 p.

Kano T. 1998. A preliminary glossary of bonobo behaviors at Wamba. In: Nishida T, editor. Comparative study of the behavior of the genus *Pan* by compiling video ethogram. Kyoto: Nissho Printer. p 39–81.

Klein, 1999. Die Sozialen Strakturen dreier Menschenattenantenim 2000. Master thesis. Westtalische Wilhelms Universität, Munster, Germany.

Kuroda SJ. 1980. Social behavior of the pygmy chimpanzees. Primates 21:181–197.

Kuroda SJ. 1984a. Interaction over food among pygmy chimpanzees. In: Susman RL, editor. The pygmy chimpanzee, evolutionary biology and behavior. New York: Plenum Press. p 301–324.

Kuroda SJ. 1984b. Rocking gesture as communicative behavior in the wild pygmy chimpanzee in Wamba, Central Zaire. J Ethol 2:127–137.

Maestripieri D. 1999. Primate social organization, gestural repertoire size, and communication dynamics. In: King BJ, editor. The origins of language: what nonhuman primates can tell. Santa Fe: School of American Research Press. p 55–77.

Malenky RK, Kuroda S, Vineberg EO, Wrangham RW. 1994. The significance of terrestrial herbaceous foods for bonobos, chimpanzees, and gorillas. In: Heltne PG, editor. Chimpanzee cultures. Harvard, England: Harvard University Press. p 59–75.

Marler P. 1965. Communication in monkeys and apes. In: DeVore I, editor. Primate behaviour field studies of monkeys and apes. New York: Holt, Rinehart and Winston. p 544–584.

Martin P, Bateson P. 1994. Measuring behaviour–an introductury guide. Cambridge: Cambridge University Press. 238 p.

McGrew WC, Tutin CEG. 1978. Evidence for a social custom in wild chimpanzees? Man 13:234–251.

Nakamura M, McGrew C, Marchant LF, Nishida T. 2000. Social scratch: another custom in wild chimpanzees? Primates 41:237–248.

Nishida T. 1970. Social behavior and relationships among wild chimpanzees of the Mahale Mountains. Primates 11:47–87.

Nishida T. 1980. The leaf-clipping display: a newly-discovered expressive gesture in wild chimpanzees. J Hum Evol 9:117–128.

Nishida T. 1987. Local traditions and cultural transmission. In: Struhsacker TT, editor. Primate societies. Chicago: University of Chicago Press. p 462–474.

Nishida T. 1990. The chimpanzees of the Mahali Mountains. Nishida T, editor. Tokyo: University of Tokyo Press.

Nishida T, Kano T, Goodall J, McGrew WC, Nakamura M. 1999. Ethogram and ethnography of Mahale chimpanzees. Anthropol Sci 107:141–188.

Patterson T. 1979. The behavior of a group of captive pygmy chimpanzees (*Pan paniscus*). Primates 20:341–354.

Pika S, Liebal K, Tomasello M. 2003. Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning and use. Am J Primatol 60:95–111.

Plooij FX. 1978. Some basic traits of language in wild chimpanzees? In: Lock A, editor. Action, gesture and symbol. London: Academic Press. p 111–131.

Plooij FX. 1979. How wild chimpanzee babies trigger the onset of mother–infant play. In: Bullowa M, editor. Before speech. Cambridge: University Press. p 223–243.

Robbins MM. 2001. Variation in the social system of mountain gorillas: the male perspective. In: Stewart KJ, editor. Mountain gorillas: three decades of research at Karisoke. Cambridge: Cambridge University Press. p 30–58.

Roth RR. 1995. A study of gestural communication during sexual behavior in bonobo (*Pan paniscus*, Schwartz). Calgary: University of Calgary Press. 1–119 p.

Savage S, Bakeman R. 1978. Sexual morphology and behavior in *Pan paniscus*. Proceedings of the Sixth International Congress of Primatology. New York: Academic Press. p 613–616.

Savage-Rumbaugh ES, Wilkerson BJ, Bakeman R. 1977. Spontaneous gestural communication among conspecifics in the pygmy chimpanzee (*Pan paniscus*). In: Bourne GH, editor. Progress in ape research. New York: Academic Press. p 97–116.

Savage-Rumbaugh ES, McDonald K, Sevcic RA, Hopkins WD, Rupert E. 1986. Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). J Exp Psychol Gen 115: 211–235.

Schaller GB. 1963. The mountain gorilla, ecology and behavior. Chicago: University of Chicago Press. 479 p.

Sugiyama Y. 1981. Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, 1979–1980. Primates 22:432–444.

Susman RL. 1984. The pygmy chimpanzee: evolutionary biology and behavior. New York: Plenum Press. 435 p.

Tanner JE, Byrne R. 1996. Representation of action through iconic gesture in a captive lowland gorilla. Curr Anthropol 37:162–173.

Tanner JE. 1998. Gestural communication in a group of zoo-living lowland gorillas Ph.D. dissertation, University of St. Andrews, St. Andrews, Scotland.

Tanner JE, Byrne R. 1999. The development of spontaneous gestural communication in a group of zoo-living lowland gorillas. In: Miles HL, editor. The mentalities of gorillas and orangutans, comparative perspectives. Cambridge: Cambridge University Press. p 211–239.

Taylor A, Goldsmith ML. 2003. Gorilla biology: a multidisciplinary perspective. Cambridge: Cambridge University Press. 528 p.

Thompson JAM. 1994. Cultural diversity in the behavior of *Pan*. In: Itani J, editor. Hominid culture in primate perspective. Niwot: University of Colorado Press. p 95–115.

Thompson-Handler NT, Malenky RK, Reinartz GE. 1995. Action plan for *Pan paniscus*. Report on free ranging populations and proposal for their preservation. Milwaukee: Zoological Society of Milwaukee County.

Tomasello M, George BL, Kruger AC, Farrar MJ, Evans A. 1985. The development of gestural communication in young chimpanzees. J Hum Evol 14:175–186.

Tomasello M, Gust D, Frost GT. 1989. A longitudinal investigation of gestural communication in young chimpanzees. Primates 30:35–50.

Tomasello M, Call J, Nagell K, Olguin R, Carpenter M. 1994. The learning and use of gestural signals by young chimpanzees: a trans-generational study. Primates 35:137–154.

Tomasello M, Call J. 1997. Primate cognition. New York: Oxford University Press. 528 p.

Tomasello M, Call J, Warren J, Frost T, Carpenter M, Nagell K. 1997. The ontogeny of chimpanzee gestural signals. In: Wilcox S, King B, Steels L, editor. Evolution of communication. Amsterdam/Philadelphia: John Benjamins Publishing Company. p 224–259.

Tomasello M, Zuberbühler K. 2002. Primate vocal and gestural communication. In: Burghardt G, editor. The cognitive animal: empirical and theoretical perspectives on animal cognition. Cambridge: MIT Press. p 293–299.

Tratz E, Heck H. 1954. Der africkanische Anthropoids 'Bonobo' eine neue Menschenaffengattring. Säugetier Mitteil 2:97–101.

Van Hooff JARAM. 1973. A structural analysis of the social behaviour of a semi-captive group of chimpanzees. In: Vine I, editor. Social communication and movement, studies of interaction and expression in man and chimpanzee. London/New York: Academic Press. p 75–162.

Vea JJ, Sabater-Pi J. 1998. Spontaneous pointing behaviour in the wild pygmy chimpanzee (*Pan paniscus*). Folia Primatol 69:289–290.

Vineberg E. 1977. Communicative patterns of behavior in a family of captive pygmy chimpanzees (*Pan paniscus*). PhD dissertation. San Diego: San Diego State University.

White FJ, Chapman CA. 1994. Contrasting chimpanzees and bonobos: nearest neighbor distances and choices. Folia Primatol 63:181–191.

Whiten A, Ham R. 1992. On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. Adv Study Behav 21:239–283.

Wrangham RW, McGrew WC, De Waal FBM, Heltne PG. 1994. Chimpanzee cultures. Harvard, England: Harvard University Press. 448 p.