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RESEARCH ARTICLE

Gestural Communication in Young Gorillas (*Gorilla gorilla*): Gestural Repertoire, Learning, and Use

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In the present study we investigated the gestural communication of gorillas (*Gorilla gorilla*). The subjects were 13 gorillas (1–6 years old) living in two different groups in captivity. Our goal was to compile the gestural repertoire of subadult gorillas, with a special focus on processes of social cognition, including attention to individual and developmental variability, group variability, and flexibility of use. Thirty-three different gestures (six auditory, 11 tactile, and 16 visual gestures) were recorded. We found idiosyncratic gestures, individual differences, and similar degrees of concordance between and within groups, as well as some group-specific gestures. These results provide evidence that ontogenetic ritualization is the main learning process involved, but some form of social learning may also be responsible for the acquisition of special gestures. The present study establishes that gorillas have a multifaceted gestural repertoire, characterized by a great deal of flexibility with accommodations to various communicative circumstances, including the attentional state of the recipient. The possibility of assigning Seyfarth and Cheney's [1997] model for nonhuman primate vocal development to the development of nonhuman primate gestural communication is discussed. Am. J. Primatol. 60:95–111, 2003.

Key words: gestures; flexibility; learning; *Gorilla gorilla*

INTRODUCTION

Communication can be defined as the transmission of information between a sender and a receiver through auditory, olfactory, tactile, and visual signals, and the subsequent use of that information by the receiver in deciding how to respond [Bradbury & Vehrencamp, 1998]. The vast majority of studies of nonhuman primate (hereafter primates) communication, both in the field and in captivity, have focused on vocal communication [e.g., Hammerschmidt & Fischer, 1998; Marler, 1976; Seyfarth et al., 1980; Snowdon et al., 1982]. Gestural

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communication has received relatively little attention, and the few relevant studies are unevenly distributed among primate species and concern mainly common chimpanzees (*Pan trologytes*). Goodall [1986] reported that wild chimpanzees in the Gombe National Park use more than a dozen distinct gestures in a variety of contexts such as play, grooming, sex, and agonism, and Plooij [1978, 1979] focused on their development. In addition, Nishida [1980] and McGrew and Tutin [1978] reported some population-specific behaviors, such as the gesture *leaf-clipping* and the *grooming hand-clasp* [but see also Boesch, 1995; Ghiglieri, 1984; Sugiyama, 1981], and claimed that they are socially transmitted [McGrew & Tutin, 1978; Nishida, 1987]. Tomasello and colleagues [1985, 1989, 1994, 1997] recorded the gestural signaling of a captive group of chimpanzees for 12 years, focusing on the learning and use of gestures.

Relatively little is known, however, about the gestural communication in the other great ape species. The major goal of the present study was to shed light on the gestural signaling of the gorilla (*Gorilla gorilla*), with a special focus on the learning and use of gestures.

Gorillas are primarily terrestrial, and the majority of groups contain one male [Doran & McNeilage, 2001] and several females with offspring, who remain together while moving and resting. Given their terrestrial and constant group cohesion, some use of visual as well as auditory communication might be expected. Descriptions of species-typical displays of wild mountain gorillas (*Gorilla beringei*) were reported by Fossey [1983] and Schaller [1963, 1964]. In addition, Parnell and Buchanan-Smith [2001] described a specific gesture, the *splash display*, used by wild western lowland gorillas to intimidate other silverbacks, and Fay [1989] observed *hand-clapping* behavior in gorilla females. Tanner and Byrne's [1996, 1999] study is the only investigation that has focused specifically on the gestural repertoire of gorillas. However, this study was conducted with only a single group of captive gorillas and focused mainly on two individuals. The investigators observed about 30 gestures, which appeared to fall into three attentional groups (variation in degree of visual attention from 39% to 100%): a high visual attention group of silent gestures, a medium visual attention group of auditory gestures, and a low visual attention group of tactile-close gestures. Each class of gestures had consistent but different communicative effects: tactile-close gestures usually resulted in movements of the receiver's body in the direction indicated by the actor, silent visually received gestures led to a high rate of bodily contact in play activity, and auditory gestures resulted in redirection of the attention or alteration of the locomotion of the recipient. These data were not tested statistically.

In terms of the learning of gestures, Tanner and Byrne [1996] claimed that ''species-typical'' expressions such as *chest-beat*, *clap*, *pound*, and *slap* are acquired by each individual. Importantly, they cited a number of cases that they considered to be iconic uses of a gesture. These gestures were performed by an adult gorilla male who seemed to signal with his hand, arm, or head to a playmate the direction in which he wanted her to move or the action he wanted her to perform (for a similar study in bonobos, see Savage-Rumbaugh et al. [1977]). However, Tomasello and Zuberbühler [2002] argued that these might simply be ritualized gestures, with the iconicity being in the eyes of the human observer only. A role for iconicity in the performance and comprehension of gestures by gorillas and other apes has not yet been properly demonstrated [Tomasello et al., 1997]. Regarding the use of gestures, Tanner and Byrne [1996] reported great variability in gestures performed by individual gorillas, including a number of idiosyncratic gestures used by single individuals

only. Importantly, they observed one gorilla that suppressed a signal by hiding her playface, and argued that this observation may illustrate the degree of neurological control that gorillas have over their hands and limbs in carrying out cognitively complex tasks, and some degree of self-conception [Tanner, 1998; Tanner & Byrne, 1993].

Elaborating on the study of Tanner and Byrne [1996], in this study we systematically describe and compare the individual gestural repertoires of 13 captive gorillas aged 1–6 years (in chimpanzees the performance of gestures declines in frequency after the age of 6 years [Tomasello et al., 1997]), with a special focus on the learning and use of gestures. The 13 subadult gorillas lived in two groups at different locations, and the similar group structure enabled us to draw within and between group comparisons.

Following other studies on gestural communication in apes [e.g., Plooij, 1978; Tanner & Byrne, 1996; Tomasello et al., 1985, 1994], we determined a gesture as expressive movements of the limbs or head, and body postures that appear to initiate a desired action (e.g., play, nurse, or ride). In addition, this study focused only on flexibly produced gestures, which are defined especially by persistence in achieving a goal, gazing at a recipient, and waiting after the performance of a signal to receive a response from the recipient [e.g., Bates, 1976; Bruner, 1981; Tomasello et al., 1989]. Therefore, gestures that appear to have a ritualized morphology (e.g., *chest beat* and *stiff stance*) are also included if they meet these criteria for flexibility.

Our first goal was to compile the gestural repertoire of the gorillas to make inferences about species-typical gestures. With regard to the learning of gestures, we focused on individual and group variability, as well as possible age-related changes in gesture use to draw comparisons and to extend the findings of Tomasello and colleagues [e.g., Tomasello et al., 1997; Tomasello & Zuberbühler, 2002] on the developmental profile of gestures in chimpanzees, as well as the main learning processes involved. Tomasello and colleagues found no evidence for a social learning process (for an overview of definitions of social learning, see recent reviews [e.g., Galef, 1988; Heyes, 1994; Whiten & Ham, 1992; Zentall, 2001]) and suggested that the main learning process involved in the acquisition of gestures is ''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]. For current purposes, the term ''social learning'' is used to indicate situations in which one individual attempts to actually reproduce or match the behavior of another [e.g., Bandura, 1986], in contrast to individual learning of social behaviors (whereby an individual learns a new behavior through reciprocal interaction (ontogenetic ritualization)). Following Tomasello and colleagues [1994], similarities among the gestural repertoires within a group, and the occurrence of 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, idiosyncratic gestures) imply that an individual learning process is involved.

With regard to the use of gestures, we examined two issues. The first concerned how flexibly the gestures were used – for instance, if the same signal was performed in different contexts and if several signals were used within the same context. Second, we investigated whether gorillas accommodate their use of gestures to the attentional state of the recipient – for example, by using visual gestures only when the recipient is looking.

METHODS

Subjects

Thirteen subadult gorillas from two family groups were observed in the Zoo Apenheul, the Netherlands, and the Howletts Wild Animal Park, United Kingdom. The name, gender, age, and location of the subjects are listed in Table I.

Zoo Apenheul, the Netherlands.

The subjects were five infant (0–3$\frac{1}{2}$ years) and two juvenile (3$\frac{1}{2}$–5 years) gorillas (the age classes are similar to those established by Fossey [1974]). In addition to those seven gorillas, the group contained one silverback, one blackback, six adult females, two nulliparous females, and one subadult female. During the day the gorillas were kept on a semi-natural island (10,000 m^2) with trees, tree trunks, bushes, a wooden climbing facility, and a water ditch. During the night they used indoor facilities (330 m^3) that contained ropes and metal climbing bars.

Howletts Wild Animal Park, United Kingdom.

The subjects were four infant and two juvenile gorillas. In addition to the six subadult gorillas, the group contained one silverback and five adult females. The gorillas had permanent access (except during cleaning hours in the morning) to indoor (200 m^3, with 18-m^3 bedrooms) and outdoor (approximately 2,600 m^3) enclosures. The floors of the gorilla enclosures were covered with straw, and the enclosures contained ropes, metal climbing bars, toys, and a slide.

Both groups were fed five to six times a day with a wide variety of different types 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 during July–October 2000 and May–July 2001 by one observer, in the public areas. The behavior of the two family groups was observed 4–7 hr per day for a total of 210 hr (15 hr per individual), using selected

TABLE I. Gorillas: Names, Gender, Age (Year and Months) and Location of the 13 Subadult Gorillas

Name	Gender	Age	Zoo
Uzuri	Male	6.2	Apenheul
Kumbo	Male	5.4	Howletts
Kihi	Male	5.4	Howletts
Bibi	Female	3.7	Apenheul
M'Bewe	Male	3.3	Apenheul
Komu	Male	3.3	Howletts
Kisiwa	Female	2.10	Apenheul
Kidjoum	Male	2.7	Howletts
Kidogo	Male	2.5	Apenheul
Kwimba	Female	1.9	Howletts
M'Kono	Male	1.8	Apenheul
M'Tongue	Male	1.7	Apenheul
Kidiki	Female	1.3	Howletts

ethological parameters. During the initial weeks, focal animal sampling [Altmann, 1974] was used to establish a complete inventory of gestures for each of the 13 subjects. Videotaping, using a digital camera (Sony DCR-TRV900E), was done on an ad libitum basis, recording continuously any and all interactions when it was possible to use the camera and when communication was likely to occur. This technique resulted in a total of 75 hr of videotape (MiniDV) of gorilla interaction.

Coding Procedure

The coding of the videotapes was done using a video walkman (Sony MiniDV, GV-DV-D900EPAL) with a slow-playback function and the coding program Interact 6518. We only coded gestures that were used to initiate (not continue) a social interaction (e.g., play, nurse, or ride) and 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: see gestural ethogram (Table II).
4. Iconic gesture: according to Tanner and Byrne [1996] the term iconic is used to refer to a gesture that depicts motion in space or the form of an action.
5. Context: a) affiliative: grooming, body contact, protection; b) agonistic: aggressive behavior such as chasing, biting, hitting, or threatening; c) food: intake of food; d) nurse: behaviors such as drinking; e) play: includes play-wrestle, play-chase, and rough-and-tumble play; f) ride: sitting on another individual's back or attempting to do so; g) travel: behaviors involving moving around in the enclosure, leaving, or arriving.
6. Attentional state of recipient: a) direct eye contact or head directed toward actor; b) head turned 90° away from actor; 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; d) action (see contexts) follows.

Reliability.

Ten percent of all coded videotapes were checked for accuracy by a second observer. The reliability test was done using Cohen's Kappa, the coefficient of which is defined on a square $r \times r$ contingency table, measuring the agreement of two independent observers, and correcting for the possibility of chance agreement. Cohen's Kappa for the agreement of the definition of gestures was 0.8, an ''excellent'' level of agreement [Altmann, 1991].

Data Analysis and Statistics

Gestural repertoire.

For the description of the gestural repertoire, only those gestures that had been observed two times in at least two individuals were included in further analysis [Tomasello et al., 1985]. Idiosyncratic gestures, which are exclusive for 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

TABLE II. Gestural Ethogram: Detailed Description of Gestures and Signal Categories.

Auditory gestures	Body beat: Animal slaps repetitively on own body part except chest with knuckles or palm of hands.
	Body slap: Animal slaps only once on own body part except chest with knuckles or palm of hands.
	Chest beat: Animal slaps repetitively on own chest with alternating open hands or knuckles.
	Clap: Palms of hands contact in space in front of body.
	Slap ground: Animal hits ground, rock, wall etc. with the palm of the hand.
	Stomp: Animal brings the sole or heel of foot suddenly and forcibly against or upon the ground, object, or walks in a pounding manner.
Tactile gestures	Embrace: Animal wraps arm/s and/or legs around the body of another animal.
	Grab: Animal grasps another animal with the whole hand; fingers are bended.
	Hand on: The palm of the hand is placed on the head of another animal and stays there >2 sec.
	Long touch: Gentle contact with flat hands, body part or feet. Duration >5 sec.
	Pull: Animal grasps another animal and forcefully moves her closer.
	Punch: Animal performs a brief forward or downward thrust on or against another animal with fist/knuckles or finger.
	Prod: Animal taps lightly and repetitively upon body part of another animal with the palm or the knuckles.
	Push: Animal uses arms to forcefully move another animal away.
	Slap: Animal comes fast from a distance and hits another animal forcefully with the palm of the hand.
	Touch: Gentle and short (<5 sec) contact with the flat hands, body part or feet.
	Grab-push-pull: Animal grabs another animal and pulls or pushes it during the same movements.
Visual gestures	Arm shake: Arm and hands are shaken loosely with rotational motion; may vary from prolonged motion of entire upper body to minimal motion of hand(s) shaken from wrists.
	Bow: Animal raises and lowers its torso by stretching and flexing the limbs alternating includes also gestures like head nod, head shake or head turn.
	Chuck up: Animal flings up its arms.
	Formal bite: Intention to bite in hands, feet or neck (open mouth and teeth are shown).
	Gallop: Animal runs very fast toward or close to another animal.
	Ice skate: Animal pirouettes with hands on the ground or in the air.
	Jump: Animal springs from or over an object close to another animal or on an animal.
	Move: Animal moves an object in front of another animal, for instance a branch, straw etc.
	Object shake: Animal joggles an object.
	Peer: Animal sits or stands very close and brings her face very close to the face of a (usually chewing) partner.
	Reach an arm: Animal stretches out an arm limb towards another animal.
	Shake: Animal moves legs/arms from side to side in front of another animal while hanging.
	Somersault: Animal makes a flip.
	Stiff stance: Animal stands with the legs held rigidly and the body stiff and erect; tight lipped face often accompanied
	Straw wave: Animal uses its hands to throw straw on its body
	Throw: Animal tosses an object toward or close to another animal.

observed the individual's current repertoire. Based on auditory, tactile, and visual components, we formed three signal categories: 1) auditory gestures that generate sound while being 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.

Age classes.

To make a direct comparison with the development of gestures in captive chimpanzees [Tomasello et al., 1997], we formed three comparable age classes (1–2, 3–4, and 5–6 years) and correlated them with the number of gestures per individual. In a cluster analysis we attempted to identify relatively homogeneous groups of cases (gorillas) based on the occurrence (yes/no) of selected characteristics (gestures), using an algorithm that started with each case in a separate cluster and combined clusters until only one was left to detect age-related changes in gesture use.

Group differences.

To assess the degree of concordance in the performance of gestures between and within the two groups, we used Cohen's Kappa statistics to determine agreement or disagreement between individuals for each gesture [c.f., Tomasello et al., 1997]. We calculated two sets of Kappas 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 in its agreement with each other individual based on a comparison of all performed gestures. These scores were then averaged across individuals to obtain group variables.

Flexibility of use.

To determine whether gorillas adjust their use of gestural signals to the attentional state of the recipient, for every gesture, the state of the recipient was coded 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

Description of Gestures and Occurrence in Contexts

By plotting the cumulative numbers of observed gestures by individual and time for all gorillas, an asymptote of gestures was reached. We concluded that we had observed the current repertoires of all 13 individuals. Overall, the gorillas performed 33 different distinct gestures (see Table II): six auditory (18%), 11 tactile (33%), and 16 visual (49%). These gestures occurred mainly in the play context (40%), but also occurred in the food (15%), riding (10%), nursing (10%), traveling (10%), affiliative (10%), and agonistic (5%) contexts.

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

Learning

To answer our questions about the learning processes involved, we performed two sets of analyses as described in the two subsections below. The

first set examined age-related changes in the variety of gestures. The second set focused on individual and group variability in the performance of gestural signals.

Age classes.

The cluster analysis did not reveal any evidence that age classes clustered due to similarities in the performance of gestures. Figure 1 displays the mean number of gestures according to three age classes. We found an increase in the mean number of gestures at the age of 3–4 years from 23 (± 3.23) to 26 gestures (± 4.36), whereas the number of gestures decreased at the age of 5–6 years to 23 (± 0.58) gestures.

Individual variability and group comparison.

Table III shows the percentage of individuals using each gesture. Eight gestures were observed in all individuals, nine in $>75\%$ of all individuals, six in 50–75%, and 10 in $<50\%$ of all individuals.

Group differences.

The analysis of the degree of concordance in the performance of gestures between and within the two groups (Cohen's Kappa statistics – see Methods) showed "excellent" strength of agreement [Altmann, 1991]. The within-group Kappas (mean $= 0.73 \pm 0.083$ for the Apenheul group; mean $= 0.85 \pm 0.1$ for the Howletts group) were similar to the between-group Kappas (mean $= 0.72 \pm 0.089$). Although the within-group Kappa was slightly higher than the between-group Kappa, an analysis of the individual Kappas of average concordance with group members and with members of the other group showed no significant difference (Wilcoxon-test: $Z = -2.271$, $P = 0.23$, $n = 12$).

We found group differences in the performance of two distinct gestures. The gestures *arm shake* and *chuck up* were specific to gorillas in the Apenheul group.

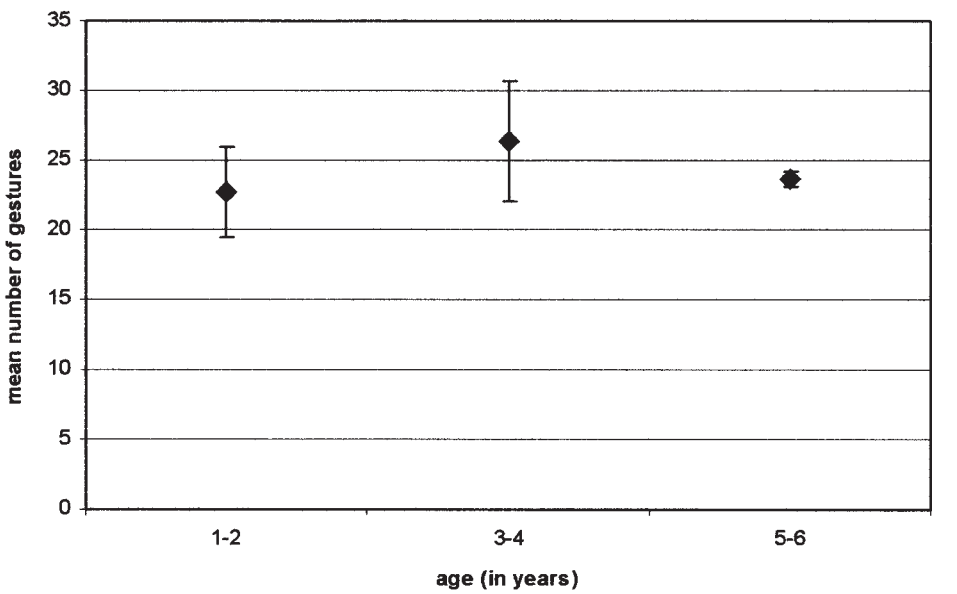

Fig. 1. Age classes. Mean number of gestures as a function of age class (1–2, 3–4, and 5–6 years). Error bars indicate the SD.

TABLE III. Performance of Gestures: Percentage of Individuals Using Each Gesture out of Each Signal Category

Auditory		Visual	
Chest beat	100%	Peer	100%
Slap ground	100%	Reach arm	100%
Body beat	77%	Formal bite	85%
Stomp	69%	Throw	77%
Clap	62%	Jump	77%
Body slap	23%	Ice skate	77%
Tactile		Gallop	77%
Grab	100%	Somersault	62%
Punch	100%	Move	62%
Slap	100%	Straw wave	46%
Touch	100%	Shake	39%
Grab-pull-push	92%	Arm shake	39%
Push	92%	Object shake	23%
Embrace	77%	Chuck up	23%
Hand on	54%	Stiff stance	15%
Pull	54%	Bow	15%
Long touch	39%		
Prod	15%		

Arm shake was performed by six of seven, and *chuck up* by three of seven individuals.

Idiosyncratic gestures.

We found three idiosyncratic gestures used to solicit play: *object drum* (an animal drums repetitively on an object with alternating hands), *object on somebody* (an animal puts an object on another individual), and *break wood* (an animal breaks wood into pieces), which were performed by three different individuals in the Apenheul group. Overall, 92.5% of these gestures occurred in the play context and received in most cases a response from the recipient in the form of an action (46.6%), such as play, or in the form of a responding gesture (20%).

Use

To answer our main questions about the flexibility of gestural use, we first examined whether one signal was used in different contexts, and whether several signals were used within the same context. Second, we tested whether gorillas accommodate their use of gestures to the attentional state of the recipient.

Table IV displays the gestures used by individuals for more than one single functional category, as well as the functional categories that were pursued with more than one gestural signal. On average each individual used 3.9 ± 2.6 gestures for more than one functional category, and on average 3.3 ± 1.0 gestures were used for the same end. With one exception, all of the gorillas used several of their signals for multiple ends, as well as multiple signals for the same end. Only one gorilla (M'Bewe) did not use any gesture for more than one functional category, but used multiple signals to request play from other conspecifics.

One signal in several contexts.

The analysis (see Fig. 2a) demonstrated that with respect to the number of all performed gestures, more than 72% of all 33 gestures were observed in more than

TABLE IV. Gestural Use: Signals Used for More Than One End per Individual and Number of Gestures Used for the Same End per Individual

	Uzuri	Kumbo	Kihi	Bibi	M'Bewe	Komu	Kisiwa	Kidjoum	Kidogo	Kwimba	M'Kono	M'Tongue	Kidiki	Total
Chest beat	X					X		X	X					4
Clap						X								1
Gallop		X	X			X								3
Grab	X	X	X	X		X	X	X		X	X	X	X	11
Grab-push-pull						X						X		2
Hand on								X						1
Move		X	X						X			X		4
Peer										X				1
Punch						X	X							2
Push				X		X		X						3
Slap								X						1
Slap ground						X								1
Somersault								X						1
Stiff stance			X											1
Throw			X			X			X					3
Touch	X		X	X		X	X	X	X	X	X	X	X	11

	Uzuri	Kumbo	Kihi	Bibi	M'Bewe	Komu	Kisiwa	Kidjoum	Kidogo	Kwimba	M'Kono	M'Tongue	Kidiki	Total (individual)
Affiliative									2					1
Agonistic	2	8	6			4	2	5	2			2		8
Food		3	3	3		4		6	2	4	2	3		9
Nurse						2								1
Play	16	17	19	17	21	23	13	22	19	21	11	20	9	13
Ride				3							2			2
Travel									3					1

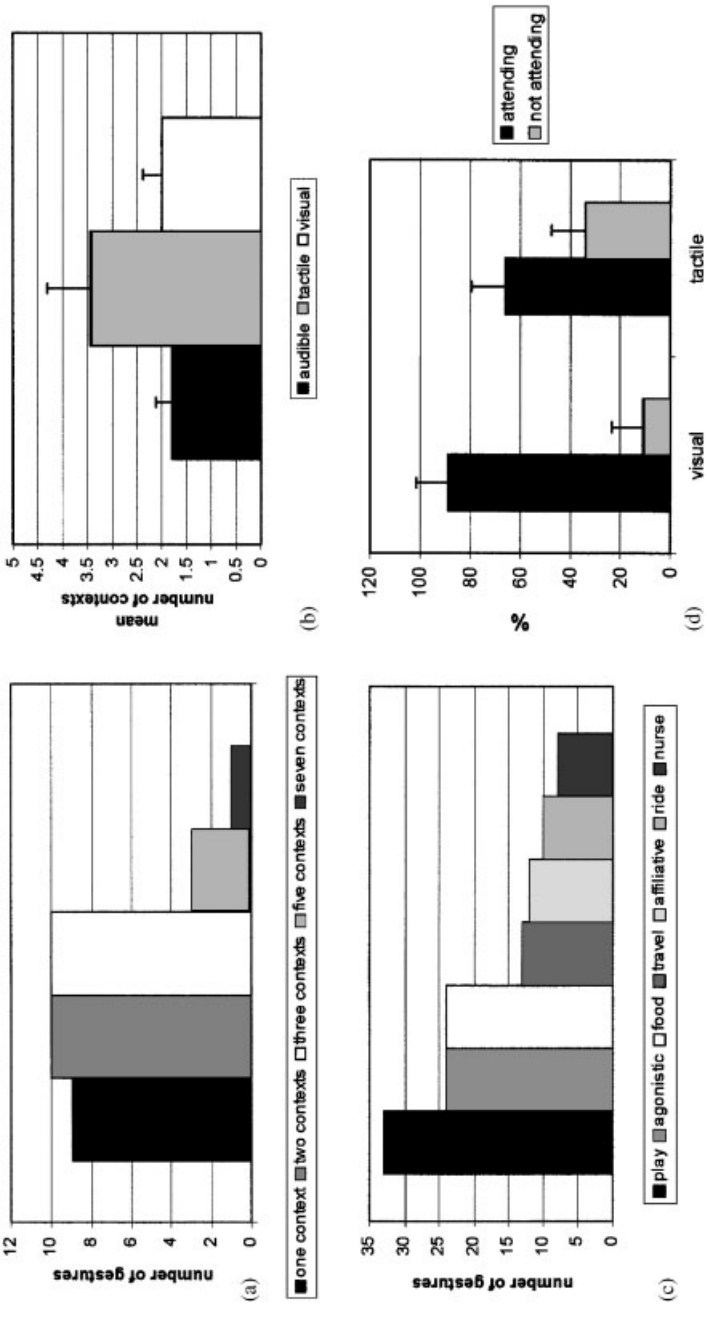

Fig. 2. Flexibility of use: (**a**) one signal is used in several contexts; (**b**) mean number of contexts in relation to the three different signal categories of audible, tactile, and visual gestures; (**c**) one context with several signals; and (**d**) adjustment to audience effects. Error bars indicate the SD.

TABLE V. Z – Values for Comparison of Different Numbers of Gestures per Context

Play vs. nurse	$Z = -5.0$	$P < 0.001$ $N = 25$
Play vs. travel	$Z = -4.472$	$P < 0.001$ $N = 20$
Play vs. ride	$Z = -4.796$	$P < 0.001$ $N = 23$
Play vs. affiliative	$Z = -4.583$	$P < 0.001$ $N = 21$
Play vs. agonistic	$Z = -3.0$	$P < 0.001$ $N = 9$
Play vs. food	$Z = -3.0$	$P < 0.001$ $N = 9$
Food vs. nurse	$Z = -4.0$	$P < 0.001$ $N = 16$
Food vs. travel	$Z = -3.317$	$P < 0.001$ $N = 11$
Food vs. ride	$Z = -3.742$	$P < 0.001$ $N = 14$
Food vs. affiliative	$Z = -3.464$	$P < 0.001$ $N = 12$
Agonistic vs. nurse	$Z = -4.0$	$P < 0.001$ $N = 16$
Agonistic vs. affiliative	$Z = -3.464$	$P < 0.001$ $N = 12$
Agonistic vs. travel	$Z = -3.317$	$P < 0.001$ $N = 11$
Agonistic vs. ride	$Z = -3.742$	$P < 0.001$ $N = 14$

one context, 27% (nine gestures) were performed in only one context, 30% (10 gestures) in two contexts and 80% in three contexts, 9% (three gestures) in five contexts, and 3% (one gesture) in seven contexts. As can be seen in Figure 2b, the mean number of contexts differed among signal categories (KW: $X_2^2 = 6.108$, $P = 0.047$). Tactile gestures occurred in more contexts, than visual gestures (MWU TAC > VIS: $Z = -2.203$, two-tailed, $P = 0.028$, $N_{tac} = 11$, $N_{vis} = 16$).

One context with several signals.

The results show that in every context, on average, approximately 18 different gestures were used. Figure 2c shows that, overall, in the play context all different gestures could be observed, whereas in the nurse context only 24% of all gestures occurred. In the agonistic and food contexts, 73% of all gestures were used, in the travel context 39% were used, in the affiliative context 36%, and in the ride context 30% were used. These differences between the occurrence of signals due to different contexts were significant for the play context vs. all other contexts and the food and agonistic contexts vs. nurse, travel, ride, and affiliative contexts among all individuals (Friedman: $x_7^2 = 121.471$, $P < 0.001$ (Fig. 2c); for Z-values of the Wilcoxon-test, see Table V).

Attentional state of the recipient (''audience effects'').

We analyzed whether the sender adjusted the performance of gestures to the attentional state of the recipient. On average, $89\% \pm 13\%$ of visual gestures occurred when the recipient was looking, whereas only $66\% \pm 12\%$ of tactile gestures occurred when the recipient was looking (see Fig. 2d). This difference was statistically significant (Wilcoxon test: $Z = -2.223$, $P = 0.026$, $n = 13$). There was no significant difference for auditory vs. visual gestures or auditory vs. tactile gestures.

DISCUSSION

The main goals of this observational study were to describe the gestural repertoire of subadult gorillas, and to investigate how gorillas learn and how they use their gestures.

We were able to compile a gestural repertoire of 33 gestures of auditory, tactile, and visual signals. In contrast to the observations of Tanner [1998], we did

not observe the gestures *arm-cross, arm-swing under*, *beat sides of head, circle hands, down, extended palm, finger down lips, foot back, hands behind back, hands between legs,* and *hide playface*. The gestures *arm-cross, armswing under,* and *extended palm* were observed in two or three individuals, but the others were idiosyncratic gestures, mainly exclusive to the female Zura (with the exceptions of *beat sides of head* (female Bawang) and *hands between legs* (male Kubie)). The gorillas of the Apenheul and Howlett groups performed gestures such as *body-slap, bow, chuck up, gallop, ice skate, jump, move, peer, shake, somersault, straw-wave, stiff stance, stomp,* and *throw* on a regular basis, and also performed the idiosyncratic gestures *object drum, object on somebody,* and *break wood*. Some of these differences might be explained in terms of individual, group, or age differences (the Tanner group had only two subadult gorillas). The main difference, however, might be explained by different rearing histories (Zura was raised by humans) and the exclusion of body postures and locomotory gaits in the current study. In addition, we observed no instances of the 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. Another explanation would be that we only observed gorillas of 1–6 years of age, whereas Tanner and Byrne [1999] suggest that gesturing of an iconic nature may be a developmental phenomenon, appearing only at adolescence and promoted by special social and physical conditions.

Concerning age classes, we found that the number of gestures used increased with age until about 3–4 years of age, after which the number of gestures declined in frequency. These findings differ from the results of Tomasello and colleagues [1997], who found in chimpanzees a gradual rise in number of gestures used until 6 years of age, increasing from six gestures on average at the age of 1–2 years to 10 gestures on average per individual at the age of 5–6 years. They argued that gestures are a more significant part of the communicative repertoire of younger chimpanzees compared to older ones, which are best thought of as ontogenetic adaptations to a set of tasks for a particular developmental period. The age differences in comparison to the present study may be due to the fact that gorillas have a shorter infancy and juvenile stage [Bogin, 1999], and appear to develop certain aspects of physical maturity and intellectual development at a younger age than do chimpanzees [e.g., Antinucci, 1990; Parker et al., 1999; Redshaw, 1978; Spinozzi & Natale, 1989]. However, further research into the gestural communication of adult gorillas is needed to confirm that gestural communication may be a more significant part of the communicative repertoire of younger gorillas compared to older ones.

With regard to the learning of gestures, we found high levels of agreement concerning the performance of gestures between groups, individual variability concerning the performance of 25 gestures, and three idiosyncratic gestures. The idiosyncratic gestures involved recurrent events in the animal's life (food and play); they were accompanied by the initiator's expectation to receive a response (indicated by response waiting), and they most often received a response in the form of an action or a responding gesture. These results imply that the idiosyncratic gestures resemble a relatively stable part of a particular youngster's gestural repertoire and were understood by other group members. Overall, these findings support (based on our defined indicators for individual learning) the hypothesis that ontogenetic ritualization is the main learning process involved. They further imply that the overlap in gestural repertoires among individuals could be accounted for by commonly available individual learning conditions.

Both groups appear to live in environments that provide similar learning conditions, triggering the acquisition of similar gestural repertoires.

However, we found group differences in the performance of two distinct gestures, which were specific to gorillas in the Apenheul group and cannot be easily explained by different physical conditions or social settings. The within-group variability in gesture use of chuck up in a given gorilla group, which was performed by three of seven individuals, appears to be of the same nature as the group variability among any groups of gorillas at any place and time. However, the existence of the gesture arm shake, which was observed in six of seven individuals in the Apenheul group but not in the Howletts group, provides evidence that for some gestures some form of social learning may play an important role.

With regard to the use of gestures, we observed that gorillas have flexible connections between signal and function. These findings are consistent with studies on chimpanzees [Tomasello et al., 1994, 1997] and siamangs (*Symphalangus syndactylus*) Liebal et al., unpublished results). In a study of 20 chimpanzees from two groups, Tomasello and colleagues demonstrated that on average each individual used 2.5 gestures for more than one function. In a study of 14 Siamangs from four groups, Liebal and colleagues found that on average visual gestures were used in 3.5 contexts, and tactile gestures were used in five contexts. In the present study, the tactile gestures also represented the most flexible gestures, showing the highest variety of functional categories, whereas auditory and visual gestures were linked to particular social contexts such as play, agonistic, and food. It seems that the communicative message of tactile gestures is quite multifaceted, whereas auditory gestures can be interpreted as attention-getting actions that draw the receiver's attention toward the signaler or the functional context, and visual gestures are more fixed to special contexts. In contrast to the nurse and ride context, in which the variety of gestures was quite low, we observed all gestural signals during play encounters. These findings fit modern theories of play, which explain the function of play as an exploration of possibilities in the environment, and exercise of movement [Fagen, 1984, 1993]. The functional category ''play'' therefore offers a platform for the exploration and practice of communicative actions that later may undergo a transformation process and acquire new functions (for chimpanzees, see Tomasello et al. [1989]).

Similar to findings of Tomasello and colleagues [1994], we found that one of the major factors affecting the choice of communicative means for gorillas in a particular situation was the attentional state of the recipient. All of the gorillas adjusted their use of visual gestures to the attentional state of the recipient, using visual gestures mainly when the recipient was looking, whereas the attention of the recipient did not play an important role in the use of tactile gestures. These results are also consistent with findings of Liebal and colleagues (unpublished results) for siamangs. Overall, the gestural communication of gorillas can be characterized by a great deal of flexibility, with accommodations to various communicative circumstances, including the attentional state of the recipient.

Until recently, only auditory gestures such as *chest beat*, *knock*, *slap*, *clap*, and *pound* were accepted as species-typical signals of gorillas. Tanner and Byrne [1999] were the first to point out that gorillas also communicate on a regular basis through tactile and visual gestures, but they focused mainly on a blackback male and a young adult female. Therefore, the present study established that subadult gorillas also use tactile and visual gestures on a regular basis, and that gestures such as *grab*, *peer*, *reach arm*, and *touch*, which were performed by all 13 individuals from two different groups (which had no direct contact with each

other), may also be an important part of the species-typical gestural repertoire of gorillas.

We found that the ability to perform these tactile and visual gestures was fully developed in infants aged 1–2 years. This result contradicts previous findings by Tanner [1998] and Redshaw and Locke [1976], who did not observe these kinds of gestures at that early age. Redshaw and Locke [1976] investigated the development of behavior in two hand-reared lowland gorilla infants that lived together without any other conspecifics. They performed the gestures *clap* and *slap* to solicit play, but chest beat occurred as a result of uncertainty and possibly anxiety, and indicated a certain degree of excitement. The gesture *slap* was always followed by the approach of the recipient. In the present study, the results for the gesture chest beat and *slap ground* were more diverse: the gesture chest beat was mainly used in play situations and the agonistic context. The gesture *slap ground* received in most cases a response in the form of a response gesture (13%) or an action (57%). These differences may be explained by different observational designs or physical and social environments, or (in the study by Redshaw and Locke [1976]) a lack of older and experienced conspecifics. Therefore, our data provide evidence that the development of a multifaceted gestural repertoire depends on the social and physical environment that creates the baseline for learning, and that exchange with group members plays an essential role.

In addition, the study by Redshaw and Locke [1976] demonstrated that even gorillas that had never seen another gorilla performing gestures developed auditory gestures, such as *slap* and chest beat. Similar observations were made by Berdecio and Nash [1981], who reported that chimpanzees from peer groups, which essentially have no opportunity to observe older conspecifics, develop many of the same play gestures as individuals from groups with more natural group composition.

These findings inspire the speculation that the production of species-typical gestures is due to genetic predisposition, triggered by commonly available individual learning conditions, while the use and response has to be learned. Seyfarth and Cheney's [1997] model for vocal development in primates suggests that vocal production, vocal usage, and responses to vocalizations develop at different rates in primates, meaning that apparently vocal production is most innate, usage is only partially under genetic control, and response is affected almost entirely by environmental cues, including social cues. Therefore, this model may also be usefully employed to examine species-typical gestural communication. Apparently, idiosyncratic gestures, which belong to the gestural repertoire of only some individuals, are acquired through ontogenetic ritualization, which confirms the hypothesis of Tomasello and Zuberbühler [2002]. However, the existence of group-specific gestures appears to support the theory of Byrne and Byrne [1993], who examined leaf-gathering skills in mountain gorilla groups at Karisoke, Rwanda. They claimed that the patterns of variation are acquired by individual learning, whereas the logical organization of the strategy is copied from others using the social-learning process known as ''program-level imitation.'' In terms of gestures, this would mean that the ''logical organization,'' the main structure of special gestures, is copied from others, but that the patterns of variation (as seen for hand use, use of objects etc.) are acquired by individual learning.

To ascertain how gestural communication develops, and whether differences within groups and among other primate species are due to social and/or ecological factors, further research, especially on wild populations in different ecological habitats, is needed.

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