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# RESEARCH ARTICLE

# Use of Gesture Sequences in Chimpanzees

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Gestural communication in a group of 19 captive chimpanzees (*Pan troglodytes*) was observed, with particular attention paid to gesture sequences (combinations). A complete inventory of gesture sequences is reported. The majority of these sequences were repetitions of the same gestures, which were often tactile gestures and often occurred in play contexts. Other sequences combined gestures within a modality (visual, auditory, or tactile) or across modalities. The emergence of gesture sequences was ascribed to a recipient's lack of responsiveness rather than a premeditated combination of gestures to increase the efficiency of particular gestures. In terms of audience effects, the chimpanzees were sensitive to the attentional state of the recipient, and therefore used visually-based gestures mostly when others were already attending, as opposed to tactile gestures, which were used regardless of whether the recipient was attending or not. However, the chimpanzees did not use gesture sequences in which the first gesture served to attract the recipient's visual attention before they produced a second gesture that was visually-based. Instead, they used other strategies, such as locomoting in front of the recipient, before they produced a visually-based gesture. Am. J. Primatol. 64:377–396, 2004. 

**Key words: gesture sequences (combinations); communication; manipulation; *Pan troglodytes***

## INTRODUCTION

Manual and bodily gestures represent a significant component of the signal repertoire in various monkey and ape species [e.g., Goodall, 1986; Liebal et al., 2004; Maestripieri, 1999; Pika et al., 2003; Tomasello et al., 1985, 1989, 1994, 1997]. As opposed to vocalizations that mostly convey context-specific information for predator avoidance or food detection, gestures are mainly used in social contexts such as playing, grooming, and nursing, and during sexual and agonistic encounters. Those contexts often represent less evolutionarily urgent functions

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than those signaled by acts of vocal communication [Tomasello & Zuberbuehler, 2002]. Thus, gestures are used in more flexible ways, as shown in previous studies by Tomasello et al. [1994, 1997]. They found that many chimpanzee gestures were individually learned (i.e., only some individuals used them). Subsequently, the gestures were used flexibly in multiple contexts, or different gestures were used in the same context interchangeably toward the same end. An important finding with respect to flexibility was that chimpanzee juveniles gave a visual signal to solicit play (e.g., ‘‘arm-raise’’) only when the recipient was already oriented appropriately. In contrast, they used their most insistent attention-getter (a physical ‘‘poke-at’’) most often when the recipient was socially engaged with others [Tomasello et al., 1994, 1997].

With regard to audience effects, Tanner and Byrne [1993] reported that a female gorilla repeatedly used her hands to hide her ‘‘play face’’ from a potential partner, indicating a possible understanding of the role of visual attention in the process of gestural communication. Kummer [1968] reported that before male hamadryas baboons set off to forage, they engage in ‘‘notifying behavior’’ in which they approach another individual and look directly into its face, presumably to make sure that the other is looking before the trek begins. A similar behavior has been reported in the context of mother–infant interactions in pigtail macaques [Maestripieri, 1996]. In an experimental setting, Call and Tomasello [1994] found that at least some orangutans were sensitive to the gazing direction of their communicative partner, and chose to not communicate when the partner was not looking at them. Hostetter et al. [2001] showed that chimpanzees also modify their communicative behavior in response to the attentional state of a human. If the human experimenter was not visually attending, auditory gestures and vocalizations were used to attract its attention and hence manipulate its attentional state, whereas visual gestures were preferred when the experimenter was attending. Therefore, audience effects in the case of primate gestural communication involve not just the presence or absence of others, but also their knowledge states (specifically, whether others can or cannot see the gesture).

There are a number of reports that nonhuman primates are not only sensitive to audience effects, and therefore modify their communicative behavior, but also that they use particular gestures to attract the recipient’s attention. For example, hamadryas baboons use ‘‘ground slaps,’’ which appear to function as attention-getters [Kummer & Kurt, 1965]. Chimpanzee youngsters often attract the attention of a partner to themselves by slapping the ground in front of, poking at, or throwing things at the desired partner when they want to initiate play [Tomasello et al., 1989]. In contrast, other gestures communicate a specific desire more directly. For example, play-hitting is an important part of the rough-and-tumble play of chimpanzees, and many individuals use a stylized ‘‘arm-raise’’ to indicate that they are about to hit the other to initiate play. Because this ‘‘arm-raise’’ signal is ritualized from actual play-hitting, its precise meaning is transparent in context (unlike the case of attention-getters). However, because it is a visually-based gesture, the recipient must be looking if the gesture is to achieve its desired end. In this regard, Tomasello et al. [1994] reported that an infant chimpanzee will often combine a visual ‘‘pout face’’ together with the tactile gesture ‘‘throw stuff’’ to make sure that its mother receives its visual request for nursing. Such a combination of gestures was also described by Nishida [1980], who found that chimpanzees use the ‘‘leaf-clipping display’’ in different social contexts to attract the recipient’s attention, which can be followed by another gesture, such as penile erection. In another study involving an experimental setting [Leavens et al., 2004], chimpanzees not only varied the modality of gestures, but also used different types of gesture combinations depending on whether a human experimenter was attending or not.

To summarize, observations of gesture sequences indicate that chimpanzees are sensitive to audience effects, and that they use particular gestures to attract the attention of others. Therefore, gesture sequences provide the opportunity to investigate whether chimpanzees manipulate the attentional state of conspecifics before using visual gestures, since such gestures require the recipient's visual attention. Gesture sequences are situations in which an individual uses more than one gesture one after another for the same end during a delimited period of time [Tomasello et al., 1994]. Since chimpanzees use gestures of several sensory modalities (visual, auditory, and tactile) this leads to a number of possible combinations, and may result in increased flexibility in the usage of a limited number of gestures. The combination of gestures may enable the sender to consider previous interactions with a particular recipient, and to adjust the communicative means depending on the recipient's state of attention and response. Persistence in communicating to force a response from the recipient, and substituting signals until the sender's social goal is obtained are both mechanisms that underlie intentional communication in humans [Bard, 1992; Bates, 1979; Bruner, 1981]. Thus, gesture sequences may represent strategies of nonhuman primates to achieve both persistence and substitution by combining gestures depending on the social goal the sender wants to obtain, and the recipient's behavior [Bard, 1992; Tomasello et al., 1985]. Interesting questions arising in this regard are whether gesture sequences are preplanned constructs, and how the recipient's behavior influences the types of gestures combined.

In the present study we investigated the use of gesture sequences in a captive group of chimpanzees. In contrast to a variety of experimental setups, this study focuses on the spontaneous and natural communicative behavior of chimpanzees interacting with their conspecifics, and addresses the following questions: 1) Which types of gesture sequences occur with respect to the number and modalities of gestures combined? 2) In which functional context are gesture sequences used? 3) How does the recipient's behavior (state of attention, responsiveness) influence the type of gesture sequence? 4) Are gesture sequences employed in ways that indicate that chimpanzees are trying to manipulate the visual attention of the recipient by using particular tactile or auditory gestures before they produce a visual gesture? In contrast to the previous studies of Tomasello and colleagues [1985, 1989, 1994, 1997], the current focus is not on the modification of the gestures themselves depending on the attentional state of the recipient, but rather on whether the sender manipulates the recipient's behavior for the purpose of communication. This would represent a much more active manipulation of attention than has previously been observed.

## MATERIALS AND METHODS

Since the current study is a follow-up investigation conducted as part of a longitudinal study lasting now almost 20 years, we used the same definitions and basic procedures of data collection and coding employed in the previous studies [Tomasello et al., 1985, 1989, 1994, 1997].

Briefly, gestures are defined as expressive movements of limbs or head and body postures used "intentionally," in the sense that 1) the sender directs a gesture toward a particular recipient, and 2) those signals show some sign of flexible use that distinguishes them from stereotyped behaviors and involuntary expressions of the internal emotional state that are not accompanied by response-waiting, persistence, or means–ends dissociation [Bruner, 1981; Sarimski, 2002; Tomasello et al., 1985, 1994]. In other words, intentional communication implies that the sender considers the recipient as a social agent, and adjusts its communicative means by augmentation, addition, or substitution of the signal until the social goal is attained [Bard, 1992; Bates, 1979].

## Subjects

A group of 19 chimpanzees were studied at the Yerkes Regional Primate Research Center (Field Station) in Atlanta, Georgia. With the exception of two individuals, all group members were born in captivity. The group was established in 1993, and subsequently all offspring born in this group were raised by their mothers (as opposed to the adults, which were previously housed at the Yerkes Regional Primate Center Main Station, where they were raised in a nursery). The group contained 10 adults (four males and six females), three subadults, five juveniles, and one infant. They were housed in an outdoor-indoor enclosure. The outdoor enclosure was $22 \times 25$ m and contained a wooden structure in the center. Various objects, such as toys, barrels, and branches, were placed throughout the compound. The chimpanzees were fed twice a day (once in the morning and once in the afternoon) with a diet of monkey chow supplemented by different types of fruits and vegetables.

## Observational Procedure

Observations took place from June through November 1999 from a platform above the outdoor enclosure. During the observations, the chimpanzees only had access to the outdoor enclosure. Since both the senior and second authors had been observers in previous studies, they trained the first author and a second person to identify the individual chimpanzees and the gestures described in previous studies. Observations were conducted by the first and second authors and the additional observer. During this initial period the observations were made together, and the criteria for defining intentional gestures were discussed so that any new gesture could be recognized as such. Regular meetings and discussions also took place during the observation period and the coding procedure. An ethogram of gestures was generated that consisted of the previously observed gestures and some other gestures that were not considered in previous studies, which served as the basis for further data collection (Table I).

In contrast to the previous studies, we used a videocamera to record the chimpanzees' interactions, and employed two methods for data collection. As in previous studies, we used ad libitum sampling to observe the group in the afternoons, two or three times per week. In addition, focal animal sampling [Altmann, 1974] was used for observations in the mornings from 8 to 12 A.M., three to four times per week. Each individual was randomly selected and videotaped for 5 min. Once the 5 min had elapsed, another subject was selected and videotaped. This procedure was repeated until all subjects had been followed once during the session. The total observation time amounted to 75 hr (33 hr of ad libitum observation, and 42 hr of focal-animal sampling).

**TABLE I. Definition of Gestures Considered in the Current Study According to Their Sensory Modality***

| Gesture | Definition |
|---|---|
| **Auditory gestures** | |
| Belly slap (bs) | Subject slaps its belly with one or two hands |
| Foot stomp (fs) | Subject puffs out its chest and approaches the other upright, stomping |
| Ground slap (gs) | Subject slaps the ground, wall, or an object with its hands |
| Hand clap (hc) | Subjects slaps its own wrist or hand |
| **Tactile gestures** | |
| Arm on (ao) | Subject approaches the other with its arm extended and places its arm on the other's back |
| Embrace (em)[a] | Subject puts one arm or both around the body of the other |
| Formal bite (fb)[a] | Subject puts its open mouth on any body part (back, neck, wrist) of the other, simulating biting |
| Gentle touch (gt)[1] | Subject puts its hand gently on any body part of the other |
| Lead (le) | Subject put its arm around the neck/body of the other and pulls it in a pretended direction |
| Lip lock (ll) | Subject sucks the others lower lip and then backs away |
| Poke at (pa) | Subject hits a body part of the other with hands, feet, or with an object |
| Pull (pu)[a] | Subject pulls on a body part (e.g., arm, leg) of the other |
| Push body (pb) | Subject pushes the body of the other away in a short, rapid movement with its hands, feet, or head |
| Push object (po) | Subject pushes an object at the other |
| Throw stuff (th) | Subject throws some loose material (stones, paper, toy, sticks) at another one |
| **Visual gestures** | |
| Arm raise (ar) | Subject raises its arm (as if to hit) |
| Arm shake (as) | Subject shakes its one hand or both repeatedly with rapid movements |
| Bipedal jumping (bj)[a] | Subject jumps upright up and down on its legs |
| Genital offer (go) | Penis: male leans back and present its genitals to the other<br>Swelling: female presents her swelling to the other |
| Head bob (hb) | Subject ''bobs and weaves'' in bowing position at the other |
| Head shake (hs) | Subject rapidly shakes head horizontally at the other |
| Offer (of)[2] | Subject presents its own body part (back, arm) in the face of another |
| Reach (re) | Subject extends its arm to the other |
| Shake object (sh) | Subject holds and rocks an object rapidly back and forth in front of its body |
| Swagger (sw) | Subject stands or sits and rocks its body from side to side |
| *Wave object (wa)* | Subject swings an object either in front of it or over its head |
| *Wrist offer (wo)* | Subject extends the back of its flexed wrist to the other |

*Abbreviations are in parentheses. Italics indicate that those gestures did not occur as part of sequences.
[a]This gesture was not considered in previous studies of Tomasello et al. [1985, 1989, 1994, 1997].
[1]''Touch side'' in previous studies of Tomasell et al. [1985, 1989, 1994, 1997].
[2]''Leg offer'', ''Back offer'', and ''Belly offer'' from previous studies of Tomasello et al. [1985, 1989, 1994, 1997] were collapsed as ''offer''.

## Coding Procedure

Videotapes were analyzed by one of the observers (the first author). For each gesture, the sender and recipient were identified, and the following variables scored: 1) gesture modality, 2) the attentional state of the recipient before each gesture, 3) the recipient's response to each gesture, 4) the functional context in which the gesture occurred, and 5) whether the gesture occurred as part of a sequence.

The gesture modality (1) was designated as a) tactile (including physical contact), b) visual (distant movements of different body parts or specific body postures), or c) auditory (nonvocal sounds). Only a few gestures represented "pure cases" of only one sensory modality. When a gesture consisted of more than one sensory modality, tactile or auditory components were preferred for classification rather than its visual component, since this gesture could still be received by a nonattending recipient. For example, "throw-stuff," which consisted of both a tactile and a visual component, was considered a tactile gesture.

A recipient's attentional state (2) was classified as a) attending (eye contact with the signaling individual or body oriented toward the sender, which is in the recipient's field of vision), or b) not attending (recipient's head is turned away from the sender, or attention is not directed toward the sender but is distracted by other social partners or incidents in the sender's environment).

The response of the recipient (3) within 5 sec after the production of a gesture was scored as a) responsive (an overt behavior, such as starting to play, or a change in the attentional state of the recipient) or b) unresponsive (the gesture led to no observable reaction from the recipient).

The different functional contexts (4) in which the gestures were used included affiliation, access (to infants or objects), agonism, food, grooming, nursing, play and sexual behaviors. Both interactions preceding and following a gesture with a focus on the recipient's response to a gesture were used to determine its function [Tomasello et al., 1997].

Two gestures were considered to be part of a sequence (5) if one sender performed them toward the same recipient and in the same context within 5 sec of each other. If one of these variables could not be coded, it was labeled as unknown.

## Statistics

Unless otherwise stated, results are presented as mean proportions. To explore whether the mean proportions of single gestures and gesture sequences were distributed differently within each functional context, we conducted paired-samples t-tests. We applied the same test to investigate whether the modality of the first gesture of a sequence varied depending on the attentional state of the recipient. The paired-samples t-test was also used to explore the types of gesture combinations depending on the recipient's response to the first gesture of a sequence. With respect to the emergence of gesture sequences, we conducted an independent-samples t-test to test for significant differences between the mean proportions of response to the different gestures depending on whether they were classified as more effective or less effective based on the median-split criterion. The independent-samples t-test was also used to investigate whether gestures that elicited a high proportion of response functioned as "attention-getters" and therefore were used significantly more often as the first gesture in a sequence compared to gestures that caused a lower proportion of response. To control for multiple comparisons, we adjusted $P$-values using the Bonferroni correction. A sequential analysis was used to detect whether there was any systematic relation between two adjacent gestures depending on the behavior of the recipient. We analyzed whether there was a relation between the recipient's mean proportion of response to gestures and the type of gesture combination used. First, we estimated the transition probability from one gesture type to another by calculating the relative frequency with which one gesture followed another.

**TABLE II. Measures of Agreement: Kappa Values and Observed Agreement Together With the Corresponding *P*-Values are shown for the different variables**

| Variable | Kappa | Observed agreement | *P*-value |
|---|---|---|---|
| Gesture modality | 0.71 | 0.92 | $P<0.001$ |
| Attentional state | 0.75 | 0.91 | $P<0.001$ |
| Response | 0.79 | 0.90 | $P<0.001$ |
| Sequence (yes/no) | 0.80 | 0.94 | $P<0.001$ |
| Length of sequence | 0.73 | 0.89 | $P=0.008$ |
| Functional context | 0.76 | 0.81 | $P<0.001$ |

Then, to test whether the transition probability of a gesture combination was different depending on the behavior of the recipient, we used Pearson's chi-squared tests to analyze 2 $\times$ 2 contingency tables. To compare several 2 $\times$ 2 contingency tables, we conducted a Breslow and Day homogeneity of odds-ratio test [Sprent & Smeeton, 2001]. All tests were two-tailed, and a null-hypothesis was rejected at an alpha level of 5%.

To assess reliability, 20% of the data were coded by a second person. Cohen's kappa was used to measure interobserver reliability across gesture modality, attentional state, response, gesture sequence, length of sequences, and the functional context. The kappa values revealed good and excellent levels of agreement [Fleiss, 1981], with an observed agreement of 81–94% (Table II).

The mean proportions of each gesture observed during focal-animal sampling and ad libitum sampling did not differ significantly (paired t-test for each gesture, all $P$-values$_{\text{corrected}}$ $\geq$ 0.088, df = 18). The same result was found for the mean proportions of functional contexts observed using the focal-animal sampling and ad libitum sampling (paired t-test for each functional context, all $P$-values$_{\text{corrected}}$ $\geq$ 0.261, df = 16). Therefore, data from focal-animal sampling and ad libitum sampling were combined for further data analysis.

## RESULTS

We recorded a total of 1,843 gestures, including 319 visual gestures (17.3%), 118 auditory gestures (6.4%), and 1,406 tactile gestures (76.3%). Approximately one-third of those gestures (34.9%, n = 643), occurred in one of the 207 sequences observed. Four sequences contained a simultaneous combination of two gestures at the same time (e.g., a "swagger" was simultaneously performed with an "arm-raise," followed by a "genital offer"). Table III shows the gestural components and frequency for each gesture sequence depending on the functional context in which it was observed for a) two-gesture sequences, b) three-gesture sequences, and c) sequences consisting of four or more gestures. To compare the characteristics of the gesture sequences and single gestures, Table IV presents a summary of single gestures as a function of gestural modality and functional context.

Figure 1 presents the proportions of sequences as a function of the number and type of gestures combined. Most sequences (62.8%, n = 130) were two-gesture sequences. The percentage of the other various gesture sequences declined sharply and steadily as the number of gestures in a sequence increased. Sequences consisting of 10 or more gestures were performed by only two different individuals: a juvenile male that insisted on performing the gesture "throw stuff" to attract a female's attention (10- and 11-gesture sequences), and

**TABLE IIIa. Two Gesture Sequences (n = 130)***

| Functional context | Gestural components | | Total frequency |
|---|---|---|---|
| Access | pa | pa | 2 |
| | pb | pb | 1 |
| Affiliation | gt | gt | 1 |
| | gt | pu | 1 |
| | of | pa | 1 |
| | pb | pb | 1 |
| Agonism | fb | sh | 1 |
| | gs | ar | 1 |
| | gs | gs | 1 |
| | gs+hs | gs | 1 |
| | gt | fb | 2 |
| | gt | gt | 1 |
| | gt | pu | 1 |
| | hs | sw | 1 |
| | pa | pa | 9 |
| | sh | sw | 1 |
| | sw | pa | 3 |
| | sw | re | 1 |
| Food | gt | gt | 1 |
| | ll | ll+pu | 1 |
| | pa | pa | 1 |
| | pu | pu | 1 |
| Grooming | gt | gt | 2 |
| Nursing | gt | gt | 2 |
| | gt | le | 1 |
| | le | pu | 1 |
| | re | pu | 1 |
| | gt | le | 1 |
| Sexual behavior | go | go | 1 |
| | go | gt | 1 |
| | gt | em | 1 |
| | gt | gt | 1 |
| | gt | pu | 1 |
| | sw | go | 1 |
| | sw | gs | 1 |
| | sw+ar | go | 1 |
| | th | th | 1 |
| Play | ao | pa | 1 |
| | ar | pu | 1 |
| | as | th | 1 |
| | bj | as | 1 |
| | fb | fb | 1 |
| | fb | pa | 1 |
| | fb | pu | 1 |
| | fs | gs | 1 |
| | fs | po | 1 |
| | gs | gs | 2 |
| | gs | pa | 1 |
| | gs | th | 1 |
| | gt | em | 2 |
| | gt | fb | 1 |
| | gt | gt | 7 |
| | gt | pa | 1 |

TABLE IIIa (*continued*)

| Functional context | Gestural components | | Total frequency |
|---|---|---|---|
| | gt | pu | 1 |
| | gt | fb | 2 |
| | hb | pa | 1 |
| | hs | gt | 2 |
| | hs | hs | 1 |
| | pa | ar | 1 |
| | pa | fb | 3 |
| | pa | gt | 2 |
| | pa | pa | 14 |
| | pa | pb | 2 |
| | pa | pu | 2 |
| | po | fb | 1 |
| | pu | gt | 1 |
| | pu | pa | 1 |
| | pu | pu | 4 |
| | sh | gs | 1 |
| | sw | gs | 1 |
| | th | pa | 2 |
| | th | th | 3 |
| | gt | gt | 1 |
| Unknown | fb | pa | 1 |
| | gt | gt | 4 |
| | hs | th | 1 |
| | pa | pa | 1 |
| | pa | pu | 1 |
| | th | fb | 1 |

*Gestural components and total frequency of each gesture sequence are shown ordered by the functional context in which they were observed. For abbreviations of gesture see Table I.

an adult male that used "poke at," "pull," and "gentle touch" to encourage another male to follow him (13-, 15-, and 39-gesture sequences). On average, adult chimpanzees performed $5.4 \pm 3.69$ sequences, subadults performed $10.3 \pm 6.81$, and juveniles performed $20 \pm 9.64$. The one infant performed 20 sequences. This corresponds to the general use of gestures (both single and in sequences) in this group: of the total of 1,843 gestures observed, juvenile individuals performed most of the gestures ($163.6 \pm 59.09$), whereas adults produced only $60.2 \pm 38.30$ gestures on average. Subadults used $87.0 \pm 34.18$ gestures, and the infant performed 145 gestures.

In general, 38.6% of all sequences were repetitions of the same gesture, with the highest proportion of those being tactile gestures (87.6%). For example, 47.7% (n = 62) of two gesture sequences, and 32.6% (n = 12) of three gesture sequences were repetitions (Fig. 1). This was also similar in sequences of four, five, and six gestures, where the proportions of repetitions ranged between 29% and 50%. Even longer sequences, such as 10- and 15-gesture sequences, were repetitions of the same (tactile) gesture, although each of those sequences was observed only once.

## Functional Context

Figure 2 shows the mean proportion of single gestures compared to gesture sequences in the different functional contexts. Individuals performed sequences

**TABLE IIIb. Three Gesture Sequences (n = 38)***

| Functional context | Gestural components | | | Total frequency |
|---|---|---|---|---|
| Access | gt | gt | gt | 1 |
| | gt | pu | pa | 1 |
| | pu | pa | pa | 1 |
| Affiliation | gt | ar | gt | 1 |
| | le | pu | of | 1 |
| Agonism | gt | gt | pa | 1 |
| | pa | pa | pu | 1 |
| Food | le | ll | gt | 1 |
| Grooming | gt | pu | pu | 1 |
| Play | ar | ar | ar | 1 |
| | as | po | pa | 1 |
| | go | hb+gs | ar | 1 |
| | gs | gs | gs | 3 |
| | gs | gs | pa | 1 |
| | gs | gs | th | 1 |
| | gs | pa | gs | 1 |
| | gs | pa | pa | 1 |
| | gt | fb | pa | 1 |
| | gt | gt | pu | 2 |
| | gt | pu | pa | 1 |
| | hc | hc | hc | 1 |
| | pa | gt | gt | 2 |
| | pa | pa | pa | 2 |
| | pb | pb | pb | 1 |
| | pu | pa | pa | 1 |
| | pu | pu | fb | 1 |
| | sw | gs | gs | 1 |
| Sexual behavior | sw | pa | pa | 1 |
| | th | go | go | 1 |
| | th | th | ar | 1 |
| | th | th | th | 3 |

*Gestural components and total frequency of each gesture sequence are shown ordered by the functional context in which they were observed. For abbreviations of gesture see Table I.

most often in the context of play (51.3% ± 30.36%) and in the agonistic context (18% ± 24.1%). In each other context such as access, food, grooming, etc., gesture sequences were represented in < 10%. We found no significant differences between the use of single gestures and gesture sequences in the eight functional contexts, (paired-sample t-test for each functional context: df = 18, all *P*-values ≥ 0.136). When we examined individual uses of each gesture, no significant differences were found with respect to the mean proportion of each gesture when used as single gesture compared to its use as part of a sequence (paired-sample t-test: df = 18, all *P*-values ≥ 0.077). However, for some gestures, differences were found with regard to the functional context they were used for as single gesture and in sequences, respectively. Thus, ''bipedal jumping'' was never observed in the functional context of access when it was performed singly, but there was one sequence in which it was combined with several ''ground slaps'' in this context. The same was true for ''head-bob,'' which was used once in the sexual context in combination with other visual gestures. ''Arm-raise'' was observed once in the affiliative context in combination with ''gentle touch.'' Finally, ''formal bite'' was repeated six times in one sequence in combination with other tactile gestures in

**TABLE IIIc. Gesture Sequences Consisting of Four and More Components (n = 39) Ordered by the Functional Context in Which They Were Observed***

| Functional context | No. | Gestural components | Total Frequency |
|---|---|---|---|
| Access | 4 | gs gs gs gs | 1 |
| | 4 | pa pb pb fb | 1 |
| | 5 | bj gs gs gs bj | 1 |
| | 5 | ll gt gt ll pa | 1 |
| Affiliation | 4 | gt gt gt gt | 1 |
| | 5 | pu po pu pu pu | 1 |
| | 7 | pu pu pu pu pu pa pu | 1 |
| | 8 | gt gt gt gt gt gt gt gt | 1 |
| | 13 | gt pu pu gt pu pu pu pu pu pb 3x pu | 1 |
| | 15 | 15x gt | 1 |
| | 39 | 13x pa pu pa pu 21x pa pu pa | 1 |
| Food | 4 | gt pu gt ll | 1 |
| | 9 | fb fb pu gt fb pu fb fb fb | 1 |
| Play | 4 | gs gs gs gs | 1 |
| | 4 | gs gs gs ar | 1 |
| | 4 | gs pa pa pa | 1 |
| | 4 | gs th bj pa | 1 |
| | 4 | pa pa pa pa | 3 |
| | 4 | po pu pu pu | 1 |
| | 4 | pu gt gt gt | 1 |
| | 5 | gs bs sw fs fs | 1 |
| | 6 | fb fb fb pb pb pu | 1 |
| | 6 | gs gs gs gs pa gs | 2 |
| | 6 | hb gt gs hb gt gt | 1 |
| | 7 | pa pa pa pa pa pa pa | 1 |
| Sexual behavior | 4 | gs th th th | 1 |
| | 4 | sw go hs hb | 1 |
| | 5 | go th th th go | 1 |
| | 5 | pa pa pa pa pa | 1 |
| | 5 | th th th th th | 1 |
| | 6 | th th th th th th | 2 |
| | 8 | po po th th th th th th | 1 |
| | 10 | th th th th th th th th th th | 1 |
| | 11 | th th go th th th th th th th go | 1 |
| Unknown | 4 | pa pa pa pa | 1 |

*The number of gestures combined (No.), the gestural components, and the total frequency of each gesture sequence are shown. For abbreviations of gesture see Table I.

the food context. Thus, four out of 207 sequences contained gestures that occurred in different functional contexts when used as single gestures compared to when they were combined with other gestures.

## Attentional State of the Recipient

To show the influence of the recipient's immediately prior state of attention on the first gesture chosen by the sender, the mean proportions of visual gestures and tactile/auditory gestures directed to attending and nonattending recipients are shown in Table V. It is important to note that for both tactile and auditory gestures, it is not essential that the recipient be visually attending, whereas this is a prerequisite for visual gestures to be perceived by the recipient. Tactile/auditory gestures were produced regardless of the attentional state of the recipient (paired-

**TABLE IV. Characteristics of Single Gestures***

| | | Functional context (%) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Modality | Gesture | Access | Affiliate | Agonistic | Food | Grooming | Nurse | Play | Sex | Unknown | Recipient attending (%) | Total frequency |
| Tactile | ao | 0 | 69.6 | 0 | 0 | 0 | 21.7 | 4.3 | 0 | 4.3 | 47.6 | 23 |
| | em | 0 | 30 | 10 | 0 | 5 | 15 | 30 | 10 | 0 | 100 | 20 |
| | fb | 13 | 7.7 | 15 | 0 | 0 | 0 | 59 | 0 | 5.1 | 78.1 | 39 |
| | gt | 3.1 | 18.4 | 5.6 | 5.6 | 9.4 | 13.1 | 35 | 1.9 | 8.1 | 47.5 | 321 |
| | le | 0 | 33.3 | 17 | 17 | 16.7 | 16.7 | 0 | 0 | 0 | 66.7 | 6 |
| | ll | 33 | 0 | 0 | 67 | 0 | 0 | 0 | 0 | 0 | 66.7 | 3 |
| | pa | 5 | 1.3 | 21 | 1.2 | 0.6 | 0 | 62 | 1.9 | 6.5 | 67.6 | 321 |
| | pb | 32 | 10.5 | 11 | 0 | 0 | 0 | 21 | 5.3 | 21 | 57.9 | 19 |
| | pu | 10 | 0 | 5.2 | 4.2 | 6.3 | 7.3 | 58 | 1.0 | 7.3 | 62.7 | 96 |
| | po | 60 | 20 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 75 | 5 |
| | th | 2.1 | 0 | 13 | 0 | 0 | 0 | 68 | 4.3 | 13 | 62.5 | 47 |
| Visual | ar | 4.2 | 0 | 0 | 0 | 0 | 0 | 79 | 12.5 | 4.2 | 73.7 | 24 |
| | as | 0 | 33.3 | 33 | 0 | 0 | 0 | 33 | 0 | 0 | 75 | 6 |
| | bj | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 100 | 9 |
| | go | 0 | 2.38 | 0 | 0 | 1.2 | 0 | 3.6 | 88.1 | 4.8 | 83.8 | 84 |
| | hb | 12 | 5.88 | 12 | 5.9 | 0 | 11.8 | 35 | 0 | 18 | 90 | 17 |
| | hs | 6.3 | 0 | 38 | 0 | 0 | 0 | 41 | 3.1 | 13 | 89.5 | 32 |
| | of | 0 | 66.7 | 6.7 | 0 | 13.3 | 6.7 | 0 | 0 | 6.7 | 100 | 15 |
| | re | 0 | 26.7 | 0 | 0 | 0 | 6.7 | 60 | 0 | 6.7 | 90.9 | 15 |
| | sh | 0 | 0 | 25 | 0 | 0 | 0 | 63 | 0 | 13 | 66.7 | 8 |
| | sw | 0 | 3.03 | 48 | 3 | 0 | 0 | 18 | 18.2 | 9.1 | 90.5 | 33 |
| | wa | 0 | 0 | 0 | 0 | 0 | 0 | 89 | 11.1 | 0 | 100 | 9 |
| | wo | 0 | 66.7 | 33 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 3 |
| Auditory | fs | 0 | 0 | 50 | 0 | 0 | 0 | 50 | 0 | 0 | 100 | 2 |
| | gs | 2.4 | 0 | 7.3 | 2.4 | 0 | 0 | 73 | 9.7 | 4.9 | 69.2 | 41 |
| | hc | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 50 | 100 | 2 |

*For each gesture, its proportional distribution across the different functional contexts, the mean percentages when it was directed towards an attending recipient, and its total frequency are shown.

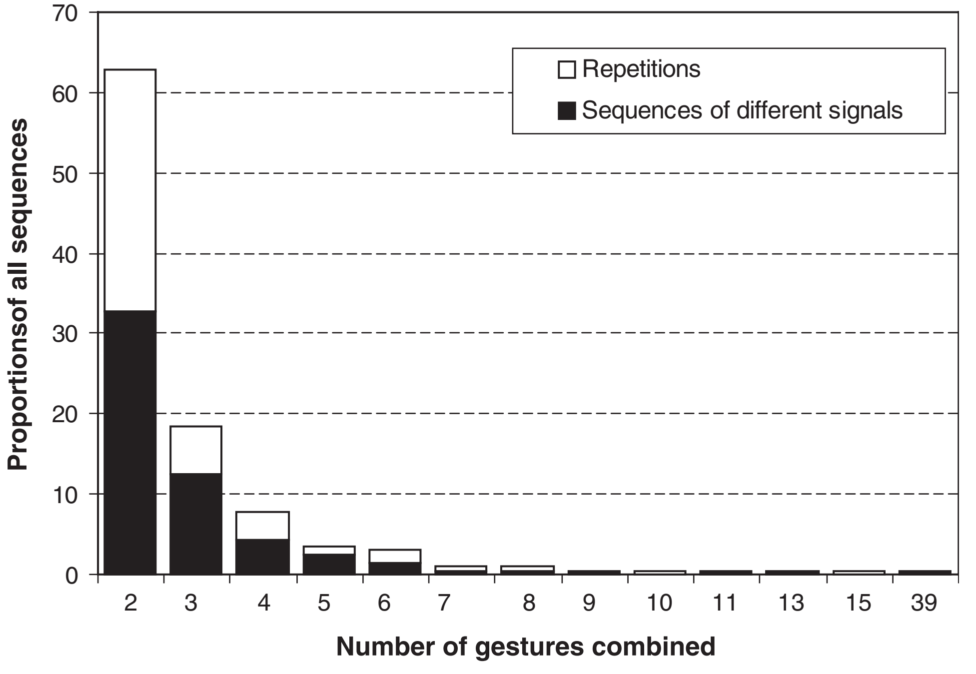


Fig. 1. Proportions of gesture sequences as a function of the number and type of gestures combined. White bars indicate the proportion of repetitions of the same gesture, while black bars indicate sequences consisting of different gestures.

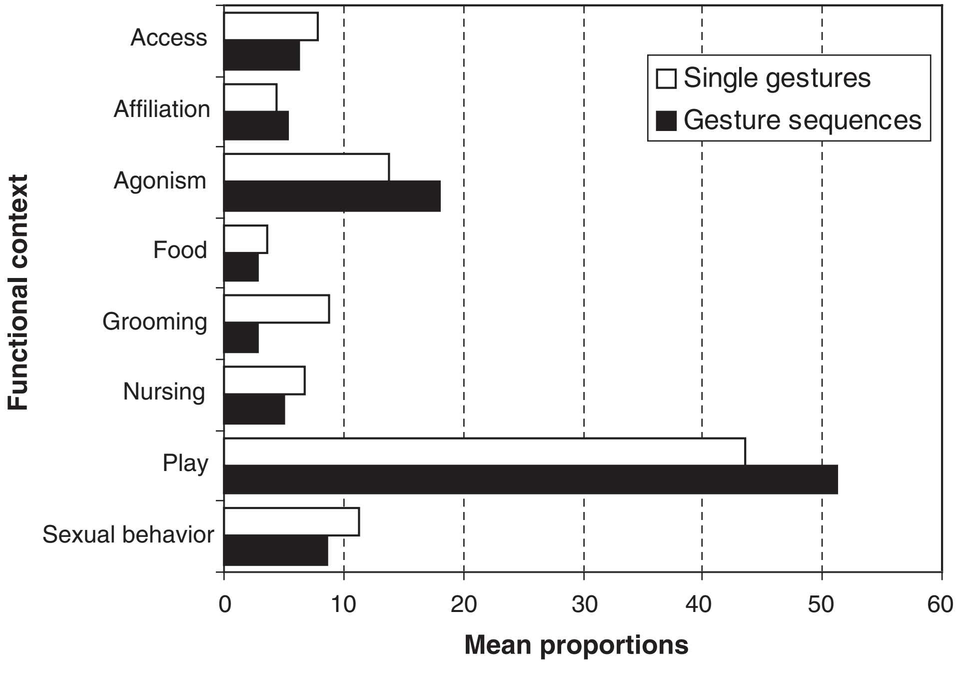


Fig. 2. Mean proportions of single gestures compared to gesture sequences used within different functional contexts.

**TABLE V: Mean Proportions (±SDs) of Tactile/Auditory and Visual Gestures, Respectively, Used As First Gesture of a Sequence Depending on the Attentional State of the Recipient***

| Attentional State | First Gesture | |
|---|---|---|
| | Tactile/auditory | Visual |
| Recipient attending (n = 111) | 84.5±17.74 | 15.5±17.74 |
| Recipient not attending (n = 72) | 95.5±12.97 | 4.5±12.97 |

*Only those cases were included where the recipient's state of attention before the performance of the first gestures was known, n = 183.

**TABLE VI. Response to Single Gestures in Context With Their Use in Sequences***

| Gesture used as | | Single gesture | Part of a sequence | | |
|---|---|---|---|---|---|
| | | | Percentage | As first gesture | As second gesture |
| | | "Less effective": response <70% | | | |
| Belly slap | (1) | – | 100 | 0 | 100[a,b] |
| Lip lock | (9) | 50.0%±70.71% | 67 | 33 | 33[a] |
| Ground slap | (105) | 55.7%±41.6% | 61 | 36[b] | 33[a] |
| Head bob | (24) | 55.7±46.4% | 21 | 40[b] | 20[a] |
| Swagger | (45) | 60.4%±45.37% | 31 | 79[b] | 14[a] |
| Offer | (17) | 61.1%±48.59% | 18 | 50[b] | 0[a] |
| Gentle touch | (442) | 62.5%±19% | 27 | 41[b] | 31[a] |
| Arm on | (24) | 64.2%±15.32% | 4 | 100[b] | 0[a] |
| Arm raise | (35) | 66.3%±20.82% | 31 | 27 | 36[a,b] |
| Shake object | (73) | 66.7%±47.14% | 4 | 67[b] | 33[a] |
| Genital offer | (97) | 68.8%±37.54% | 13 | 31 | 38[a,b] |
| Pull | (166) | 69.1%±36.39% | 40 | 19 | 39[a,b] |
| Embrace | (23) | 70.0%±48.3% | 13 | 0 | 100[a,b] |
| | | "More effective": response >70% | | | |
| Head shake | (39) | <74.1%±25.15% | 21 | 75[a,b] | 13 |
| Arm shake | (9) | 75%±50% | 33 | 67[a,b] | 33 |
| Bipedal jumping | (12) | 80.0%±44.72% | 33 | 50[a,b] | 0 |
| Poke at | (495) | 81.1%±12.08% | 35 | 29[a] | 32[b] |
| Formal bite | (67) | 81.9%±24.06% | 41 | 25[a] | 50[b] |
| Reach | (17) | 83.3%±35.36% | 18 | 50[a] | 50 |
| Throw stuff | (124) | 87.6%±0 16.5% | 61 | 22[a] | 25[b] |
| Push body | (33) | 85.0%±33.75% | 42 | 21[a] | 43[b] |
| Hand clap | (6) | 100.0%±0% | 50 | 33[a] | 33 |
| Lead | (11) | 100.0%±0% | 45 | 60[a,b] | 40 |
| Foot stomp | (6) | 100%±0% | 67 | 50[a,b] | 0 |
| Push object | (12) | 100.0%±0% | 58 | 43[a] | 57[b] |

*The total frequency of each gesture is shown in parentheses. Gestures are arranged according to the mean proportion (±SD) of response they elicited as single gestures (more or less than 70%, respectively). Percentages indicate how often each gesture was part of a sequence (calculated as percentage of its total frequency) and how often it was used as first and second gesture, respectively (shown as percentages of its total frequency in sequences).
[a]Indicates at which part of a sequence an either 'more' or 'less effective' gesture was expected to occur.
[b]Indicates where they were actually observed more frequently.

sample t-test: t(13) = –0.249, $P$ = 0.807). Even if the recipient was attending, a tactile/auditory gesture was chosen significantly more often as the first gesture of a sequence (84.5%±17.74%) compared to visual gestures (15.5%±17.74%) (paired

**TABLE VII. Choice of Second Gesture If There Was No Response of the Recipient to the First Gesture***

| Repetitions (n = 69) | | Other gesture of the same modality (n = 28) | | Switch to different gesture modality (n = 16) | |
|---|---|---|---|---|---|
| Auditory: | 11.9% ± 25.2% | Auditory: | 7.4% ± 24.4% | Auditory → tactile: | 9.7% ± 25.92% |
| Tactile: | 75.5% ± 37.7% | Tactile: | 57.9% ± 48.38% | Auditory → visual: | 5.6% ± 23.6% |
| Visual: | 1.4% ± 4.3% | Visual: | 12.5% ± 32.37% | Tactile → visual: | 1.4% ± 5.89% |
| | | | | Visual → auditory: | 5.6% ± 23.6% |
| | | | | Visual → tactile: | 22.2% ± 39.19% |
| Total | 58.5% ± 27.03% | | 28.7% ± 25.49% | | 12.9% ± 24.23% |

*Results are shown as mean percentages ± SD (only those sequences were included where there was no response after first signal, n = 113).

t-test: t(15) = 7.512, $P_{corrected} < 0.001$). When the recipient was not attending, the sender chose a tactile/auditory gesture 95.5% ± 12.97% of the time, and visual gestures only 4.5% ± 12.97% of the time. Thus, visual gestures were used significantly more often if the recipient was attending compared to when it was not attending (paired t-test: t(13) = –2.876, $P_{corrected} = 0.039$).

## Emergence of Gestures

Given that the majority of visual gestures were only produced if the recipient was visually attending, and that some gestures only rarely elicited a response from the recipient when used singly (see Table VI), we investigated whether gestures were combined in a premeditated fashion to raise their efficiency. Thus, less-effective gestures (i.e., with a low proportion of response elicitation) might be preceded by more-effective gestures so that the recipient's attention would be directed toward the less-effective gesture. Based on the median-split criterion, we divided the scores of mean response to single gestures into two groups by calculating the median proportion of response out of all single gestures, which was 70%. Those gestures below 70% were classified as less effective, while those gestures above 70% were classified as more effective (Table VI). It was expected that low-effective gestures would be used more frequently as the second gesture in a sequence. However, no significant differences were found between the proportions of gestures used as the second gesture depending on whether it was classified as more or less effective (independent-samples t-test: t(22) = –0.009, $P = 0.993$). In other words, less-effective gestures were not used particularly often as the second gesture in a sequence to be supported by a preceding, more-effective gesture.

Support for this result comes from a sequential analysis of the first two gestures of each sequence. The transition probability that a more-effective gesture would be followed by a less-effective gesture was only 0.21. Furthermore, if the first gesture was less-effective and the recipient did not respond, the transition probability that this gesture would be combined with a more-effective gesture was only 0.22. Although there were significant differences depending on whether there was a response to the first gesture (Breslow-Day test: $\chi^2_7 = 4.11$, $P = 0.043$), in both cases the sequences of two more-effective gestures one after another were observed more often than predicted by chance (Pearson $\chi^2$ test for no response: $\chi^2_7 = 44.31$, $P < 0.001$, transition probability = 0.85; Pearson $\chi^2$ test for response: $\chi^2_7 = 11.959$, $P = 0.001$, transition probability = 0.71).

### Attention-Getter

Another analysis showed that more-effective gestures, which elicited a response $>$ 70% of the time when used as a single gesture, were not used significantly more often as the first gesture in a sequence compared to less-effective gestures (independent-samples t-test: $t(18.6) = 0.861$, $P = 0.4$). Furthermore, none of the more-effective gestures, regardless of whether they were performed as a single gesture or as the first gesture in a sequence, were used significantly more often if the recipient was not attending compared to when it was attending (paired-samples t-test: all $P$-values$_{\text{corrected}} \geq 0.451$, df = 16 for single gestures; all $P$-values $\geq 0.166$, df = 15 for sequences). These results suggest that more-effective gestures did not serve as attention-getters.

### Response

To analyze whether the types of gestures combined were a function of the recipient's behavior, we calculated the mean proportions of response toward the first gesture of a sequence. On average, the recipient responded only 45.8% $\pm$ 31.07% of the time to the first gesture of a sequence compared to 74.9% $\pm$ 15.02% of response to single gestures, which was a significant difference (paired-samples t-test: $t(22) = 3.935$, $P = 0.001$). This supports the conclusion that chimpanzees did not combine their gestures in a premeditated fashion to increase the efficiency of the gestures, but rather they combined them in a serial fashion when the recipient did not react appropriately to the first gesture.

Support for this interpretation comes from another analysis, which focused on gesture sequences in which there was no response from the recipient after the sender's first gesture. Table VII details these data in terms of the gesture modalities of the first and second gestures of a sequence. The sender repeated the same gesture (most often tactile gestures) significantly more often (58.5% $\pm$ 27.03%) than it chose another gesture of the same or different gesture modality (28.7% $\pm$ 25.49% and 12.9% $\pm$ 24.23%, respectively; paired-samples t-test: repetitions vs. two different gestures of the same modality: $t(17) = 3.28$, $P_{\text{corrected}} = 0.012$; repetitions vs. two gestures of different modalities: $t(17) = 3.28$, $P_{\text{corrected}} < 0.001$). When the sender switched to a different gesture modality, it most often combined a visual gesture with a tactile gesture (22.2% $\pm$ 39.19%). Thus, although the chimpanzees were able to adjust their communicative strategies on some occasions, and chose another gesture if there was no response, most often they repeated the same or a similar gesture when the recipient did not respond. Therefore, both the low proportion of response to the first gesture and the high proportion of repetitions appear to indicate that the second gesture was instigated by this lack of responsiveness.

### Manipulation of the Attentional State

Independently of the recipient's attentional state, four different types of gesture combinations were observed: 1) tactile/auditory gesture followed by another tactile/auditory gesture (86.1% $\pm$ 13.38%), 2) tactile/auditory gesture followed by a visual gesture (1.8% $\pm$ 4.31%), 3) visual gesture followed by another visual gesture (3.2% $\pm$ 5.55%), and 4) visual gesture followed by a tactile/auditory gesture (9% $\pm$ 11.90%). Since visual gestures require the attention of the recipient, and it was shown that chimpanzees are sensitive to the recipient's state of attention, we analyzed whether chimpanzees manipulate the attentional state of the recipient by using a tactile/auditory gesture first to set up a second visual of gesture – particularly if the recipient is not attending. Therefore, the type 2 of gesture combination (tactile/auditory gesture followed by a visual gesture) was expected when the recipient was initially not attending but changed its attentional state after the production of the first gesture in the sequence. However, in only eight sequences did we observe that the attentional state of the recipient changed from not attending before the first gesture to attending after the first gesture. In those eight instances, we observed the expected type of gesture combination (tactile/auditory gesture followed by a visual gesture) in only one instance, whereas in the other cases a tactile/auditory gesture was combined with another tactile/auditory gesture.

Although the chimpanzees were sensitive to the recipient's state of attention, they did not manipulate its attentional state by using a particular attention-getter before performing a visual gesture, but merely repeated the same gesture again. One possible reason for these negative results is that the sender may have used some other strategy to obtain the recipient's attention. Therefore, we analyzed the sender's behavior before it used visual gestures. We found that the sender directly approached the recipient and then started to perform a visual gesture 25.7% of the time, or that it walked around the recipient to be within its range of vision (14.3%) if the recipient was not attending. A more passive strategy was that the sender would start to gesture if the potential recipient was approaching him, or turned around and was now facing him (12.4%). These behaviors, which are similar to the "notifying" behavior of baboons, illustrate once again that chimpanzees know when others can and cannot see them, and that if they can not be seen by a recipient there is no point in producing a visually-based gesture. Thus, chimpanzees do indeed take active steps to secure the attention of another on some occasions; however, rather than using gestures to manipulate the attention of the other, they are attempting to manipulate the behavior of the partner directly.

## DISCUSSION

The present study was intended as a follow-up to previous research concerning gestural communication in a captive group of chimpanzees, with a focus on the chimpanzees' production of gesture sequences. In this regard, we investigated whether chimpanzees use particular gestures to attract a recipient's attention before performing visual gestures. Unlike other studies addressing the use of attention-getters and adjustments of the gesture modality to the attentional state of a human recipient [Hostetter et al., 2001; Theall & Povinelli, 1999], this study investigated the natural communicative behavior between conspecifics. The present study also provides a detailed description of the gesture sequences that allowed us to analyze the chimpanzees' communicative behavior depending on both the attentional state and response of the recipient.

The most general findings were as follows: About one-third of the recorded gestures were part of a gesture sequence, confirming the findings of Tomasello et al. [1994]. The majority of gesture sequences (almost two-thirds) consisted of only two gestures (most often tactile gestures). Almost 40% of the gesture sequences were repetitions of the same gesture, and more than half of all sequences occurred in the context of play. No significant differences were found with respect to the use of gesture sequences compared to single gestures across the different functional contexts. However, some gestures were used in sequences within a different functional context compared to when they were performed as single gesture. However, it is difficult to generalize from these few examples that chimpanzees combine gestures to create "new meanings," since these instances were rare. Furthermore, the function of a gesture is defined by the context in which it is used, rather than a gesture itself having a particular meaning.

With respect to the question of how gesture sequences emerge, it is important to emphasize that the term "premeditated" does not necessarily mean that chimpanzees plan an entire gestural sequence before they execute it. However, based on previous experience in a particular context or with a particular individual, they may know that some gestures rarely cause a response and therefore must be preceded by another gesture that serves to draw the recipient's attention toward the sender. Nevertheless, gesture sequences resulted most frequently from situations in which the first element of the sequence failed to get a response. This suggests that chimpanzee gesture sequences may not be premeditated constructions, but rather are post hoc responses to an unresponsive recipient. This would also explain the high number of repetitions (instead of choosing another more efficient gesture as the second element) even if the recipient was unresponsive to the initial gesture.

With respect to the differential use of gesture sequences as a function of the recipient's state of attention (audience effects), our main finding was that the chimpanzees very seldom used visual gestures when the recipient was not already attending. This replicates the previous findings of Tomasello et al. [1994, 1997]. Hostetter et al. [2001] observed in an experimental setting that chimpanzees modified their gestures and vocalizations according to the attentional state of a human experimenter, indicating that chimpanzees can also distinguish a human's attentional state. Theall and Povinelli [1999] used a similar paradigm to investigate the use of nonvisually-based gestures and vocalizations depending on the attentional state of the human recipient, but they found no evidence that the frequency and temporal patterning of the chimpanzee's communicative behavior was affected by the degree to which the human was visually attending to them. Although attention-getting behavior was frequently observed, chimpanzees did not use those gestures significantly more often if the human experimenter was not visually attending. This is consistent with the findings of the present study, considering the communicative behavior observed between conspecifics. Theall and Povinelli [1999] argued that chimpanzees' attention-getting behaviors are deployed without being mediated by an explicit understanding of the internal attentional state of the recipient, but that their knowledge is largely governed by the general posture of others, particularly the orientation of the face. At first glance, the negative findings of the present study appear to support this argument, since there was no evidence that the chimpanzees performed gesture sequences to manipulate the attentional state of the recipient. However, there may be some restrictions on the interpretation of the present data. First, the manipulation of the attentional state of others may play a more important role in wild chimpanzees living in a relatively much more structured environment, with dense vegetation and therefore a restricted range of vision. Second, the rather short focal bouts may have been insufficient for us to observe gesture sequences. However, this objection can be ruled out, since two gestures were considered as part of a sequence only if the time interval between them did not exceed 5 sec. Finally, the present data set may be limited given that in almost two-thirds of the sequences, the recipient was already attending when the sender started to perform the first gesture. Thus, it may be that the expected pattern was not frequently observed because there was no need to attract the recipient's attention first.

Another reason for the negative findings may be that chimpanzees don't manipulate a behavior by gestures, but use other interesting strategies to make sure that the recipient is attending before the sender starts to produce visual gestures. Thus, the chimpanzees moved around in front of the recipient and gave their visual gesture there instead of using gestures to attract its attention. In the experimental studies of Theall and Povinelli [1999] and Hostetter et al. [2001], the chimpanzees were not able to alternate their position in relation to the body orientation of the human experimenter. This may have influenced the results such that other strategies to obtain the recipient's attention were not likely to occur based on the experimental design. It might be more appropriate to examine this issue in an experimental setup in which the body orientation of the human experimenter varies in relation to the chimpanzee, but the subjects are given a choice as to whether they move around to face the experimenter or they stay behind him and use gestures to attract the human's attention. It was recently found in such an experiment that chimpanzees and other great apes preferred to move around to face a human experimenter before gesturing than to call attention to themselves by using tactile or auditory signals [Liebal et al., 2004]. Thus, apes are not only sensitive to the orientation of humans, they can also modify their spatial location so that others can see them. This result highlights the importance of combining experiments with observations of the natural behavior of the species under study. Without the observational data, one might conclude that chimpanzees do not modify the perceptual experiences of recipients.

In conclusion, the present results suggest that chimpanzees do not use gestures to manipulate the attention of others with respect to the second gesture; rather, they use other strategies to make sure that the recipient sees the sender performing visual gestures. Thus, chimpanzees are aware of what others can and cannot see, and use this information to gesture effectively. In accordance with some recent analyses of monkey vocalizations [Owren & Rendall, 2001], these findings suggest that the goal of chimpanzee communication signals is to manipulate the behavior (and not necessarily the attentional or mental states) of others.

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