Anim Cogn
DOI 10.1007/s10071-012-0587-6

ORIGINAL PAPER

Use of gesture sequences in captive chimpanzee (*Pan troglodytes*) play

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Received: 20 September 2011 / Revised: 4 December 2012 / Accepted: 10 December 2012

Abstract This study examined the use of sensory modalities relative to a partner's behavior in gesture sequences during captive chimpanzee play at the Chimpanzee and Human Communication Institute. We hypothesized that chimpanzees would use visual gestures toward attentive recipients and auditory/tactile gestures toward inattentive recipients. We also hypothesized that gesture sequences would be more prevalent toward unresponsive rather than responsive recipients. The chimpanzees used significantly more auditory/tactile rather than visual gestures first in sequences with both attentive and inattentive recipients. They rarely used visual gestures toward inattentive recipients. Auditory/tactile gestures were effective with and used with both attentive and inattentive recipients. Recipients responded significantly more to single gestures than to first gestures in sequences. Sequences often indicated that recipients did not respond to initial gestures, whereas effective single gestures made more gestures unnecessary. The chimpanzees thus gestured appropriately relative to a recipient's behavior and modified their interactions according to contextual social cues.

Keywords Gestural communication · Attentional state · Chimpanzee · Gesture sequence

Introduction

Numerous studies have examined the use of strings of multiple gestures, or *gesture sequences*, by large-bodied apes. For example, Tomasello and colleagues (1994) found that captive juvenile chimpanzees used gestures both singly and in combinations. In that study, chimpanzees used about 30 % of their gestures in combination with other gestures, most often in a play context. Typically, these combinations occurred when an individual used a play gesture, and the recipient did not respond, which resulted in the individual gesturing again with the same or a different gesture. Later, Liebal et al. (2004a) also found that chimpanzees use gesture sequences in dyadic interactions. They similarly found that the greatest proportion of both single gestures and gesture sequences occurred in the play context. Although gesture sequences frequently occur during play, chimpanzees also gesture in other behavioral contexts including agonism, threat, reconciliation, sex, grooming, greeting, reassurance, and feeding (Fouts et al. 1984; Goodall 1986; McGrew and Tutin 1978; Nishida 1980; Roberts et al. 2012a, b).

Liebal et al. (2004a) examined how chimpanzees use sequences of gestures relative to the attentional states of partners. In this study, chimpanzees used visual gestures more frequently when the recipient was attending rather than looking away. In contrast, they used tactile and auditory gestures regardless of the recipient's attentional state. If the partner was not attending, they typically moved to a location where the recipient could see them before using visual gestures. More recently, Genty and Byrne

Electronic supplementary material The online version of this article (doi:10.1007/s10071-012-0587-6) contains supplementary material, which is available to authorized users.

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Published online: 23 December 2012

(2010) analyzed gesture sequences in three zoo-living groups and one free-living population of western gorillas (*Gorilla gorilla gorilla*). Gesture actors did not produce sequences because recipients were unresponsive to initial gestures. Combinations of multiple gestures did not increase the likelihood of recipient response. Instead, gesture sequences in gorillas were often used in play, and these play gestures may have initiated and regulated play interactions between individuals. Hobaiter and Byrne (2011a) examined gesture sequences in free-living chimpanzees, including both rapid-fire gesture 'sequences' (with pauses of less than 1 s between gestures, similar to Genty and Byrne 2010) and gesture 'bouts', which allowed response-waiting pauses of up to 5 s between gestures (as per Liebal et al. 2004a). They found that free-living chimpanzees used both sequence types, with rapid-fire 'sequences' emerging to regulate social interactions and response-waiting 'bouts' emerging with unresponsive recipients. Older individuals relied more on single gestures, perhaps because they had learned which gestures were more effective in eliciting a response. Finally, Roberts et al. (2012a, b) defined gesture sequences as gestures occurring within 30 s and the same behavioral context. They also found that free-living chimpanzees used gestures singly and in sequences.

The present study examined the use of gesture sequences in conspecific interactions among chimpanzees at the Chimpanzee and Human Communication Institute (CHCI). This group uses species-specific gestures as well as acquired American Sign Language (ASL) signs to communicate with humans and each other (Fouts et al. 1984; Jensvold and Gardner 2000; Leitten et al. 2012). Several studies have demonstrated that these chimpanzees gesture appropriately relative to the attentional state of their partner (Bodamer and Gardner 2002; Krause and Fouts 1997). Using methods and statistical analysis procedures similar to those of Liebal et al. (2004a) and Genty and Byrne (2010), this study explored the chimpanzees' use of play gestures with regard to a recipient's attention and responsiveness. This study is unique in several respects, however. Since a number of previous studies found by far the highest proportion of gestures and gesture sequences in the play context (Genty et al. 2009; Hobaiter and Byrne 2011a; Liebal et al. 2004a; Tomasello et al. 1994), the present study examined gesture sequences in this context only. Liebal et al. failed to examine the role of vocalizations and mouth sounds (non-vocal sounds produced with the mouth, for example, Bronx cheers and kiss sounds), but in other research chimpanzees vocalized differentially based on the attentional state of a recipient (Bodamer and Gardner 2002; Hostetter et al. 2001). Therefore, this study examined vocalizations and mouth sounds in addition to gestures.

This study also differs from previous studies in that it focused on cross-fostered chimpanzees raised in an enriched environment much like that of a deaf human child (see 'Method' section and Gardner and Gardner 1989 for more details on rearing conditions for this chimpanzee group). Gardner and Gardner (1994) described the positive influence of the cross-fostering environment and an ethological research approach on the communicative richness and frequency, as well as ASL sign utterance length, of this chimpanzee group. Thus, although not a primary focus of this study, we expected possible differences in gesture sequence length and frequency in this chimpanzee group relative to other studied captive groups. We hypothesized that the chimpanzees' use of gesture modalities, vocalizations, and mouth sounds would vary relative to the attentional state and responsiveness of the recipient. In particular, we hypothesized that the chimpanzees would use visual gestures primarily toward attentive recipients, and auditory and tactile gestures, vocalizations, and mouth sounds primarily toward inattentive recipients. Further, we hypothesized that gesture sequences would be more prevalent toward unresponsive rather than responsive recipients of initial gesture attempts.

Methods

Participants

The group of five chimpanzees at CHCI was observed for this study. This group included three females, Washoe, Moja, and Tatu, and two males, Dar and Loulis. From 1981 to May 6, 1993, these chimpanzees lived in a 27.87-m^2 facility on the third floor of the psychology building of Central Washington University. Washoe was born in Africa, while Moja, Tatu, Dar, and Loulis were all born in American laboratories.

Washoe, Moja, Tatu, and Dar were cross-fostered in human homes. Cross-fostering occurs when the offspring of one species is raised by the adults of another species (Gardner and Gardner 1989; Stamps 2003). These chimpanzees were raised in an environment like that of a deaf human child and acquired signs of ASL in this environment (see Gardner and Gardner 1989 for additional details of the chimpanzees' rearing). The fifth chimpanzee, Loulis, was raised by Washoe from the age of ten months onward and acquired many of his ASL signs from Washoe, and the other chimpanzees to whom he was exposed. See Fouts et al. (1982, 1989) for more details on Loulis' rearing and ASL sign acquisition.

Procedure

Adventitious video coding

Data were collected from adventitious videotapes of the chimpanzees. Adventitious videotapes were typically recorded during special events such as holiday parties and birthdays. As a result, they did not systematically focus on particular individuals for specified time intervals. During recording, camera operators focused primarily on ASL conversations, chimpanzee social interactions, and object manipulation. Additionally, camera operators recorded events like foraging, play bouts, private signing, and agonistic encounters. We chose these videotapes because they contained many examples of gesture sequences. They contained interactions between multiple chimpanzees, especially in the social play context, when gesture sequences tended to occur in high frequency in another group of chimpanzees (Liebal et al. 2004a). In addition, these videotapes included audible recordings of chimpanzee vocalizations and noisy gestures, which were crucial to this study. We coded these videotapes in three phases of video analysis.

The first phase of video analysis was to identify behavioral contexts. Data collectors sampled a total of 87 adventitious videotapes recorded from 1985 to 1993. They reviewed each videotape and coded the occurrence of all behavioral contexts in each minute. For example, one coded minute contained affinitive social, play, feeding, and object manipulation contexts. This phase was necessary as only minutes coded with social play were included in subsequent analyses. The Ethogram of Behavioral Contexts had been established previously and is detailed in the *CHCI Taxonomy of Chimpanzee Behaviors* (see Electronic Supplementary Material). Data collectors extracted all instances of social play identified in the first phase of the analysis. This resulted in a list of minutes that contained social play. Data collectors coded instances of play gestures in the selected minutes.

In the second phase of video analysis, data collectors identified gestures during social play instances. Gestures were defined as 'all discrete, non-locomotor limb and head movements, regardless of the receptive sensory modality (sight, sound, touch) that occurred when (chimpanzees) were in proximity and engaged in social interaction immediately before, after, or during the movements' (Tanner and Byrne 1999, p. 216). Data collectors categorized specific play gestures according to the Ethogram of Play Gesture Types, listed in the 'Appendix' section. We developed this ethogram using preliminary observations of play gestures at CHCI and play gestures defined by Liebal et al. (2004a). We defined each gesture type according to its placement, configuration, and movement. Placement identified where the gesture occurred, configuration identified the configuration of the body part involved in the gesture, and movement identified the action of the body part during the gesture (Stokoe et al. 1965; Tanner and Byrne 1996). Data collectors coded gestures in each social play segment by their name and time of occurrence. Occasionally, non-play gestures occurred in the middle of a gesture sequence. For example, some social play bouts switched to another context, such as threat or agonism, before returning to play within the same minute. To preserve sequences, we retained these non-play gestures while recording their context of occurrence. When analyzed separately, however, this small gesture set displayed similar patterns of use to play gestures. Nonetheless, we excluded these non-play gestures from most subsequent analyses, except reports of overall descriptive statistics.

In the third phase of video analysis, data collectors coded gesture sequences. For each gesture identified in the second phase, data collectors coded the following variables: gesture actor, behavioral context, modality, gesture recipient, recipient attentional state, recipient responsiveness, whether or not the gesture occurred as part of a sequence, and vocalizations/mouth sounds. We defined gestures as occurring in a sequence if one actor performed two or more gestures toward the same recipient within 5 s of each other (Liebal et al. 2004a). See Table 1 for descriptions of each variable and its categories.

We ensured that data collectors achieved acceptable inter-observer reliability for each phase of video analysis. During the first phase of analysis, numerous data collectors learned to code videotapes for behavioral context, since behavioral context-coded video is used for numerous research projects at CHCI. The first author and one additional reliable data collector coded data for the two subsequent phases of data coding. For each phase of video coding, researchers created reliability tests from videotaped segments. To create test keys, two observers independently coded the tests and compared results. Their scores were at least 85 % in agreement. After scoring the tests, they discussed disagreements and agreed on codes. Prospective data collectors coded reliability tests and obtained a score of at least 85 % for each variable prior to beginning data collection. If a data collector obtained a score below 85 % for any variable, they continued to take tests until they achieved a score of at least 85 % for all variables before proceeding with data collection.

Analysis

We calculated proportions for gesture modalities, types, and use singly and in sequences. We also calculated gesture sequence lengths. For these descriptive statistics, we pooled observations across all five chimpanzees.

Table 1 Gesture sequences variables and categories

Variable and category	Description
Gesture actor	The chimpanzee who made the gesture
Gesture recipient	The individual who the actor looked toward, oriented toward, or gestured toward
Gesture modality	
Tactile	The gesturing individual made contact with the recipient, either through direct contact or through the use of an object which touched the recipient (e.g., a piece of hose)
Auditory	The gesture was audible (but not vocal) and did not make physical contact with the recipient (e.g., a clap)
Visual	The gesture was neither audible nor made physical contact with the recipient
Recipient attentional state	
Attending	Recipient directed eye contact, face orientation, or body orientation toward the actor when the gesture was made
Not attending	Recipient directed eye contact, face orientation, and body orientation away from the actor when the gesture was made
Recipient responsiveness	
Responsive	Within 5 s following the end of a gesture, the recipient displayed an overt behavioral response to the gesture, such as an open palm slap or a change in orientation toward the actor
Unresponsive	Within 5 s following the end of a gesture, the recipient displayed no overt behavioral response

Table 2 Summary of variables and categories

Variable	Category
Modality	Auditory/tactile
	Visual
Attentional state	Attending
	Not attending
Recipient responsiveness	Responsive
	Unresponsive
Recipient attentional state shift	Attending → attending
	Attending → not attending
	Not attending → attending
	Not attending → not attending
Actor effectiveness shift	More effective → more effective
	More effective → less effective
	Less effective → more effective
	Less effective → less effective
Actor modality shift	Visual → visual
	Visual → auditory/tactile
	Auditory/tactile → auditory/tactile
	Auditory/tactile → visual

For subsequent analyses as described below, however, we relied on mean proportions based on individual scores from each of the chimpanzees to avoid non-independence of data. Relevant patterns of gesture use often were similar between individuals and differences, where present, are discussed in the Results. For most comparisons described below (except where noted otherwise), we used single-samples *t* tests based a null hypothesis of equiprobability between groups. Where appropriate, we attempted chi-square tests and Wilcoxon signed-ranks tests. Because of low cell values, however, these tests were often inappropriate. Additionally, ANOVAs were avoided due to inequality of variances.

Attentional state and modality

We tested whether the modality of the first gesture in a sequence was dependent on the recipient's initial attentional state. Responses to visual gestures require a recipient's visual attention, but neither auditory nor tactile gestures require a recipient's visual attention. Thus, we combined auditory and tactile gestures. We limited this analysis to the first gesture of each sequence and the initial attentional state. Table 2 shows the modality variable, the attentional state variable, and the categories within each variable. We compared modality use when recipients were either attentive or inattentive (see also Liebal et al. 2004a).

Responsiveness: single gestures versus gesture sequences

We tested whether recipients responded more to single gestures than first gestures in sequences (Liebal et al. 2004a). Table 2 shows the recipient responsiveness variable and the two possible responsiveness categories. We also tested the likelihood that actors would produce a second gesture based on recipient responsiveness to an initial gesture. Next, we tested whether certain gesture types were used more frequently than expected singly versus in sequences (Genty and Byrne 2010). We only included gesture types used more than 20 times in this analysis. We used a median split criterion to distinguish between gesture types used more often than expected singly and in sequences. The median split criterion separated the data into two sets—gestures used than more than expected singly and those used more than expected in sequences—based on the median percentage of use in sequences across all included gesture types. We then compared mean effectiveness of gestures used more than expected in sequences to those used more than expected singly. This allowed us to determine whether gestures used more than expected singly are more effective than those

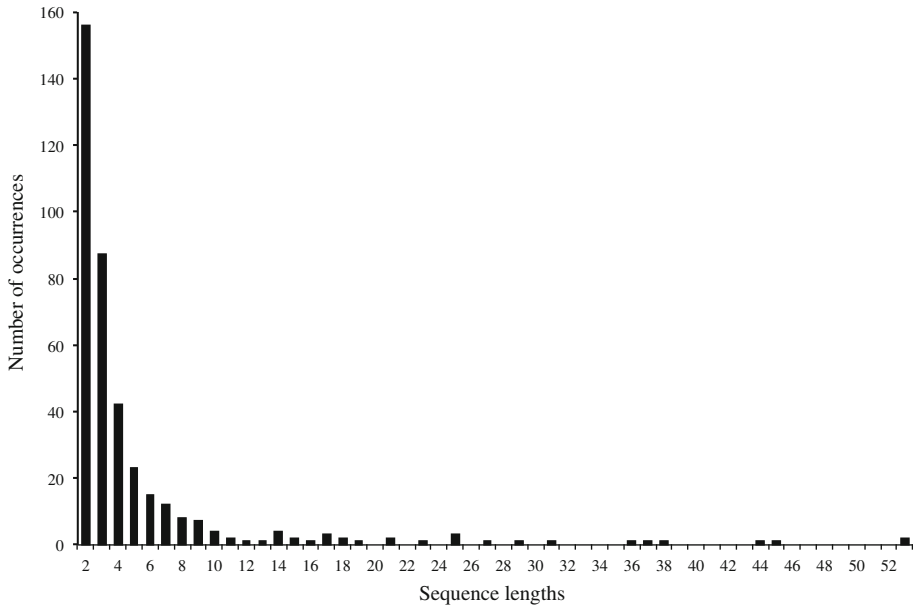

Fig. 1 Number of occurrences of each gesture sequence length

Table 3 Summary of play gesture modality and recipient's attentional state

Gesture modality	Attentional state				
	Attending		Not attending		Total
	No.	%	No.	%	
Auditory/tactile	159	79.5	100	88.2	259
Visual	35	20.5	7	11.8	42
Total	194		107		301

Percentages listed are the mean percentages for all actors

used more than expected in sequences (and thus reduce the need to produce further gestures).

Recipient responsiveness to shifts in gesture effectiveness and modality

We examined actor responses to ineffective gestures by calculating the proportion of ineffective gestures followed by: (1) no response within the 5 s following gesture production, (2) the same gesture, or (3) a different gesture (Genty and Byrne 2010). We then tested whether actors shifted gesture effectiveness or modality in response to ineffective initial gestures. To test this, we classified gestures into two effectiveness types: more effective (MEG) and less effective (LEG) (Hobaiter and Byrne 2011a; Liebal et al. 2004a). To calculate effectiveness, we first identified all gesture types that occurred five or more times as single gestures. There were 12 gesture types that fit this criterion. For each of these gesture types, we calculated a percentage of total uses as a single gesture that evoked a response. We then used a median split criterion to classify these gesture types as either MEG or LEG. Table 2 shows the four possible effectiveness shift categories under the actor effectiveness shift variable. We compared mean percentages for which actors used the same gesture effectiveness type versus switching effectiveness types for the first two gestures in sequences. We also did this comparison for modality types for the first two gestures. In addition, we analyzed whether the modalities of the first two gestures in sequences shifted relative to the recipient's initial responsiveness. Table 2 shows the four possible modality shift categories under the variable of actor modality shift. These analyses were limited to the first two gestures in each sequence regardless of the total sequence length.

Results

The 500 min of selected adventitious video yielded a total of 2,552 gestures. Of these gestures, over three quarters (1,986 gestures, 77.8 %) appeared in sequences. Overall, there were 1,980 tactile gestures (77.6 %), 282 visual gestures (11.0 %), and 239 auditory gestures (9.4 %). There were 387 sequences. Sequence lengths ranged from 2 to 53, with a modal length of 2 (Mean = 5.13, Mdn = 3). Figure 1 shows the number of occurrences of each gesture sequence length.

Vocalizations occurred in conjunction with 79 gestures. These vocalizations were food grunts (45), laughter (27), aggressive barks (2), screams (2), soft barks (2), and a pant grunt (1). Food grunts occurred in conjunction with play gestures because social play was often recorded during forages in the chimpanzees' enclosures. These vocalizations occurred before, during, and after the occurrence of

the gestures and were not associated with changes in the attentional states of recipients. Mouth sounds such as Bronx cheers and kisses were never recorded in the 5 s prior to and following gestures.

There were a total of 28 gesture types. The most frequently observed gesture types were grasp (20.3 %), open palm slap (16.1 %), and object use (10.4 %). There were 29 ASL signs, including BLACK, CHASE, HUG/LOVE, HURRY, and THAT.

Attentional state and modality

When the recipient was initially attending during play, all actors most frequently used an auditory/tactile gesture. Similarly, when the recipient was initially inattentive during play, all actors most frequently used an auditory/tactile gesture and rarely used a visual gesture. Actors were significantly more likely to use auditory/tactile rather than visual gestures in sequences when recipients were initially attending (79.5 vs. 20.5 %, $t(4) = 5.35$, $P = .01$). They were also significantly more likely to use auditory/tactile rather than visual gestures in sequences when recipients were initially inattentive (88.2 vs. 11.8 %, $t(4) = -5.25$, $P = .01$). Thus, actors were more likely to use auditory/tactile rather than visual gestures regardless of the recipient's initial attentional state. There was, however, a trend toward more auditory/tactile gestures with inattentive recipients and more visual gestures with attentive recipients. The chimpanzees rarely used visual gestures toward inattentive recipients (7 of 42 visual gestures, see Table 3). Recipients were equally likely to be attending or not attending when actors first used either an auditory/tactile gesture or a visual gesture (auditory/tactile, 79.5 vs. 88.2 %, visual, 11.8 vs. 20.5 %, $t(4) = 1.86$, $P = .14$). Table 3 summarizes the recipients' initial attentional states and the actors' subsequent gesture modalities.

Recipients rarely shifted their attentional state in response to the initial gesture. They were most often attending before and after the initial gesture, which was most often auditory/tactile. Recipients also were most often attending before and after visual gestures. All recipients displayed a similar pattern of attentional shifts relative to the initial gesture modality.

Responsiveness: single gestures versus gesture sequences

Recipients responded significantly more to a single gesture than to the first gesture in a sequence (78.0 % responsive to single gestures, 67.5 % responsive to first gestures, paired-samples t test, $t(4) = -4.23$, $P = .01$). Additionally, actors produced a second gesture less often when recipients responded to the first gesture in a sequence. Actors produced a second gesture in an average of 35.3 % of instances when recipients responded to an initial gesture attempt, versus 49.9 % of instances when recipients did not respond to an initial gesture attempt, a difference which approached significance (paired-samples t test, $t(4) = 2.63$, $P = .06$). Overall, then, actors more often used sequences when recipients were initially unresponsive than when they were responsive. Thirteen gesture types occurred often enough for their relative frequency in sequences versus singly to be analyzed. The median use in sequences for these gesture types was 87.8 %. Seven gesture types occurred more than expected in sequences, based on the median split criterion: open palm slap (379 in sequences vs. 32 singly), back hand thump (212 vs. 4), punch (150 vs. 3), poke at (145 vs. 6), foot stomp (132 vs. 8), kick (72 vs. 10), and knuckle drum (39 vs. 2). Similarly, six gesture types occurred more than expected as single gestures: grasp (300 in sequences vs. 219 singly), object use (152 vs. 114), reach (80 vs. 44), push body (59 vs. 13), and ASL (9 vs. 20). The mean responsiveness percentage for gestures used more than expected in sequences was 60.8 %. In contrast, the mean responsiveness for gestures used more than expected singly was 71.8 %. This difference was not statistically significant (Mann–Whitney test, $N_1 = 7$, $N_2 = 6$, $U = 29$, $P > .05$), but the direction of difference supports the finding above that gestures used singly are more effective and thus lessen the need to use additional gestures.

Recipient responsiveness to shifts in gesture effectiveness and modality

We examined the behavior to follow an actor's unsuccessful gesture attempt. Of 219 ineffective initial gestures, 111 (50.7 %) were followed by no additional gestures within 5 s, 70 (32.0 %) were followed by the same gesture, and 38 (17.3 %) were followed by a different gesture. We examined the relationship between effectiveness shifts and responsiveness more closely. The median response percentage for the 12 included gesture types was 83.4 %. Table 4 shows the gesture types that met the selection criterion, their response percentages, and effectiveness classifications. Overall, actors began sequences more frequently with MEGs than LEGs. All actors most frequently used two consecutive MEGs when recipients were initially responsive. Tatu, Moja, and Loulis most often used two consecutive MEGs when recipients were initially unresponsive, while Washoe and Dar most commonly used two consecutive LEGs. As a group, the actors used the same effectiveness for each of the first two gestures significantly more often than they switched effectiveness (84.0 vs. 16.0 %, $t(4) = 12.21$, $P < .01$). Table 5 shows the percentages in which each actor used the same effectiveness

Table 4 Gesture types and their effectiveness

Gesture type	Response (%)	Effectiveness classification
Kick	100	MEG
Push body	91.7	MEG
Kickback	85.7	MEG
Grasp	84.7	MEG
Open palm slap	84.4	MEG
Object use	84.3	MEG
Reach	82.5	LEG
Head bounce/sway	80	LEG
Poke at	66.7	LEG
American sign language	61.1	LEG
Arm tag	57.6	LEG
Foot stomp	57.1	LEG

MEG more effective gesture, *LEG* less effective gesture

versus switched effectiveness for the first two gestures and mean percentages overall.

All actors most frequently used two consecutive auditory/tactile gestures when recipients were initially responsive. The same was typically true when recipients were initially unresponsive. The exception was Tatu, who preceded an auditory/tactile gesture equally often by auditory/tactile and visual gestures when recipients were unresponsive. Table 6 shows the percentages in which each actor used the same modality versus switched modalities for the first two gestures and mean percentages overall. As a group, the actors used the same modality for each of the first two gestures significantly more often than they switched modalities (75.9 vs. 24.1 %, $t(4) = 4.41$, $P = .01$). Tatu, however, used the same modality only slightly more often than she switched modalities.

Discussion

Gesture modality and recipient attentional state

Actors used gesture modalities appropriately relative to the attentional states of their communicative recipients. In particular, actors rarely used visual gestures when recipients were inattentive, similar to Hobaiter and Byrne (2011b) and Liebal et al. (2004a). They frequently used auditory and tactile gestures when recipients were inattentive as well as attentive. Vocalizations were not associated with shifts in recipient attention, and mouth sounds were not observed in conjunction with gestures. This finding was like Hobaiter and Byrne (2011b), who similarly found that audible gestures were not associated with recipient attention.

Table 5 Gesture effectiveness for the first two gestures in a sequence

Actor	Same effectiveness (%)	Switch effectiveness (%)
Loulis	93.2	6.8
Dar	85.2	14.8
Washoe	85.1	14.9
Tatu	78.6	21.4
Moja	77.8	22.2
Overall mean	84.0	16.0

Table 6 Gesture modalities for the first two gestures in a sequence

Actor	Same modality (%)	Switch modalities (%)
Loulis	88.6	11.4
Moja	83.3	16.7
Dar	81.3	18.7
Washoe	70.6	29.4
Tatu	55.6	44.4
Overall mean	75.9	24.1

A number of previous studies provide evidence that chimpanzees vary their gesture modalities relative to the attentional state of a recipient (e.g., Bodamer and Gardner 2002; Hobaiter and Byrne 2011b; Hostetter et al. 2001; Krause and Fouts 1997; Leavens et al. 2004; Liebal et al. 2004a, b; Russell et al. 2005; Tempelmann et al. 2011; Tomasello et al. 1994). Why, then, might the results of the current study as well as Liebal et al. (2004a) indicate that chimpanzees use auditory and tactile gestures regardless of a recipient's attentional states? We propose several explanations. First, auditory and tactile gestures are effective with both attentive and inattentive recipients. Thus, their use is appropriate with a recipient of any attentional state. Indeed, the CHCI chimpanzees showed a trend toward more auditory and tactile gestures with inattentive recipients, but possibly because of the high overall frequency of tactile gestures, this trend did not reach significance. This trend is supported by Hobaiter and Byrne's (2011b) finding of more tactile gestures with inattentive recipients. Perhaps more importantly, they rarely used visual gestures with inattentive recipients. This is especially meaningful, since visual gestures are ineffective toward inattentive recipients.

The chimpanzees' frequent use of tactile gestures in particular may reflect the nature of play. Social play is often highly tactile. Rough-and-tumble play, characterized by contact between play partners, is present in many primate species and across human cultures (Fry 2005). In addition, repetitive behaviors are considered a defining feature of play (e.g., Bekoff and Byers 1981), which may help explain the finding that the chimpanzees are significantly more likely to repeat (rather than switch) gesture

modality and effectiveness type for the first two gestures in sequences. The importance of tactile, repetitive behaviors to the play context may outweigh the tendency for chimpanzees to modify gesture modality and effectiveness with regard to recipient attention. Instead, chimpanzees may be more likely to alter their gesture modalities in other, less inherently tactile and repetitive behavioral contexts. Future studies could focus on the relationship between gesture modalities and attentional states in other behavioral contexts, such as affinitive social, where high levels of contact are less likely.

In addition, captive constraints may influence chimpanzee gesture modality. Both Liebal et al. (2004a) and the current study examined communicative interactions between conspecifics rather than between chimpanzees and human caregivers. Captive settings typically limit social interactions between chimpanzees and their human caregivers because enclosures create physical barriers that restrict contact between gesture actor and recipient. Leavens and Bard (2011) also provide discussion of the role of the captive environment in gesture use. Thus, chimpanzees use auditory gestures, vocalizations, and mouth sounds as critical attention-getting mechanisms when interacting with human caregivers. Krause and Fouts (1997) and Bodamer and Gardner (2002) found a strong tendency for the CHCI chimpanzees to use auditory gestures and mouth sounds toward inattentive human caregivers separated by an enclosure barrier. Numerous other studies (e.g., Hostetter et al. 2001; Leavens et al. 2004; Tempelmann et al. 2011) have demonstrated a similar tendency in captive apes.

Indeed, when chimpanzees can move relative to a human caregiver, their gesturing patterns adjust accordingly. In Liebal et al. (2004b), researchers examined how orangutans, gorillas, chimpanzees, and bonobos modified their gestures based on the orientation of an experimenter and the location of food. The experimenter led the apes into a testing room where they could gesture through holes in a Plexiglas partition to obtain food. The apes could freely move to the sides and either the front or back of the experimenter, depending on the experimenter's orientation in a given trial. In all conditions, chimpanzees and bonobos (but not gorillas and orangutans) produced significantly more visual gestures to the front of the experimenter. They typically did not use auditory or tactile gestures to gain the experimenter's attention. Auditory and tactile gestures were less prevalent in this study than in others, most likely because the apes did not need to rely upon these modalities as attention getters.

An even less restrictive environment is one in which chimpanzees interact with conspecifics in social groups. In this environment, chimpanzees can incorporate tactile gestures into their interactions and can move into the visual field of a recipient before gesturing. They need not rely heavily on auditory gestures, vocalizations, and mouth sounds toward inattentive recipients. In Liebal et al. (2004a), chimpanzees did not use auditory or tactile gestures to gain the attention of inattentive recipients before using visual gestures. Instead, they often moved into the visual fields of inattentive recipients prior to using visual gestures. Similarly, Hobaiter and Byrne (2011b) and Roberts et al. (2012b) found that auditory gestures were relatively infrequent in a free-living chimpanzee community, suggesting a possibly reduced reliance on such gestures in the absence of physical barriers. The present study did not measure movement into an inattentive recipient's visual field. A follow-up study with this data set, however, revealed few instances of actors moving into the visual field to gain a recipient's attention prior to gesturing. The high frequency of tactile gestures in this study, however, suggests that during play with a proximate conspecific partner, rough-and-tumble tactile gesture use is the contextual preference. Thus, a recipient's attentional state is one of numerous factors affecting an actor's gesture modality choice. Additional factors such as behavioral context and the proximity of social partners also play important roles.

Gesture use and recipient responsiveness

Actors also demonstrated appropriate gesture use relative to the recipient's responsiveness. They were significantly more likely to use gesture sequences rather than single gestures toward initially unresponsive recipients. In addition, gestures that were used more than expected singly had a higher mean effectiveness than those that were used more than expected in sequences. Together, these findings provide evidence that gesture sequences often indicated that a recipient did not respond to an initial gesture. If recipients were initially responsive, additional gestures may have been unnecessary and were less often used. These findings are similar to those of Liebal et al. (2004a) and Roberts et al. (2012b) and suggest that gesture sequences occur, at least in part, because of a recipient's lack of response to initial gesture attempts. In contrast, Genty and Byrne (2010) assert that gesture sequences instead function to regulate interactions.

We suggest that these possibilities are not mutually exclusive. While the initiation of a gesture sequence may often begin as a response to an ineffective single gesture, the sequence may continue even after gestures produce a response. While the role of gesture sequences in modulating play behaviors was not the focus of this study, there is reason to believe they may help serve this function. The presence of sequences containing as many as 53 gestures is most likely not due simply to a repeated attempt to produce a response in recipients. Indeed, an examination of the 13

longest sequences in the data set (all sequences containing 25 or more gestures) revealed that only 1 sequence never produced a response from the recipient. All other sequences produced at least one response, and this response was not limited to the final gesture of the sequence. This suggests that even after some gestures effectively produced a response, sequences continued, perhaps in order to regulate play interactions. Play signals can help to continually clarify the behavioral context, since play and aggressive behaviors often show a great degree of overlap (e.g., Brown 1988). Thus, play gesture sequences may function both as a response to ineffective single gestures (at least initially) and also to regulate social play between partners. Additional support for this explanation comes from Roberts et al. (2012b), who found that chimpanzees repeat or elaborate subsequent gestures in a sequence, thereby showing persistence. Hobaiter and Byrne (2011a) also found that the use of both gesture 'sequences' and 'bouts' was best explained by interaction regulation and persistence, respectively (see 'Introduction' section). Although our study adhered to Liebal et al.'s (2004a) definition of gesture sequences, our findings also suggest that sequences may emerge both with unresponsive recipients and to regulate social interactions.

Gesture use: an ethological approach

Overall, then, our results suggest that captive chimpanzees produce gestures and gesture sequences frequently and appropriately under naturalistic captive conditions. These findings contrast with those of some other studies of captive ape gesture use (e.g., Kaminski et al. 2004; Povinelli and Eddy 1996; Reaux et al. 1999; Theall and Povinelli 1999) and highlight the importance of naturalistic social conditions for revealing communicative aptitudes. Johnson and Karin-D'Arcy (2006) suggest that an ethological approach, which provides the rich context of natural social interactions, is a necessary prerequisite for attentional recognition abilities to become evident. King (2007) describes ape gestural communication as a continuously molded interaction between two individuals, resting not on the individual behaviors of actors and recipients but rather on the units of meaning that are created as the interaction unfolds between participants. The cross-fostering environment in which the CHCI chimpanzees grew up encouraged natural and spontaneous communication. The chimpanzees have interwoven ASL into a rich repertoire of communicative behaviors which also includes chimpanzee gestures, vocalizations, and facial expressions. Their conversations with each other and human caregivers are not restricted by artificial testing environments and procedures. In the present study, these naturalistic social conditions allowed the chimpanzees to demonstrate their recognition of the attentional states and responsiveness of communicative recipients. Additional studies could examine the chimpanzees' recognition of attentional states and responsiveness in their use of other communicative behaviors. These studies will undoubtedly continue to illustrate the necessity of an ethological approach to understanding the complex social interactions of our next of kin.

Acknowledgments We thank Jessie Haight, Nicholas Helble, Holly Moskowitz, Erika Nelson, Lorraine Smith, and Sophia Smith for assistance with data collection and entry. For assistance with video archive use, we thank Jason Wallin. We also thank Stephen Lea, Catherine Hobaiter, and one anonymous reviewer for helpful comments on an earlier draft of our manuscript. This research was generously supported by the Central Washington University Office of Graduate Studies and Research.

Appendix

See Table 7.

Table 7 Ethogram of play gesture types

Gesture type	Placement (P)	Configuration (C)	Movement (M)
Arm around	On body of recipient	Arm slightly bent and extended toward recipient	C extends toward and wraps around P
Arm flail	In front of or beside recipient	Extended arm	C is moved in a rapid up-and-down motion toward P
Arm raise	Above the actor's head	Arm extended from body	C is lifted up quickly to P
Arm tag	Body of recipient	Bent arm extended from shoulder	C contacts P
American Sign Language (ASL)	Standard ASL placement of the sign	Standard ASL configuration of the sign	Standard ASL movement of the sign
Back hand thump	Surface around actor	Arm bent at the elbow, top of forearm oriented away from the actor	C extends from body and forearm or wrist hits P
Block	Area around the head and body of actor	Arm is raised and bent	C moves to P and is held there briefly
Elbow	On body of recipient	Arm is bent with elbow facing recipient	C moves toward and contacts P
Embrace	On body of recipient	Arms bent and encircling	C wraps around P
Foot clap	Area around the actor	Both legs extended from body, bottoms of feet facing each other	C brought together in an audible clap
Foot stomp	On floor or other surface	Actor sits or stands with leg slightly extended from body, foot parallel to floor	C lifts up and then is drawn back down to the ground so the foot slaps P
Foot tag	On body of recipient	Leg is bent or extended with a flexed or pointed foot	C contacts P
Grasp	On body of recipient	Curved, clasping hand	C closes around P
Head bounce/ sway	Looking or oriented toward recipient	Upright head, seated or quadrupedal posture	Head moves in up-and-down or side-to-side motion
Hit	On cage or recipient	Arm is extended toward cage or recipient	C moves toward and forcefully contacts P
Kick	On body of recipient	Leg bent or extended toward recipient	C forcefully contacts P
Kickback	Area around recipient	Leg extended up in the air behind actor, bent at the knee	C kicks behind actor and toward P
Kiss	On body of recipient	Pursed lips	C contacts P and held there briefly
Knuckle drum	Surface near recipient	Fingers curled under, palm oriented toward recipient	Backs of knuckles of one or both hands tap P repeatedly
Object use	Area surrounding recipient	Holding object with hand, foot, or mouth	Object is manipulated, thrown, flailed, or tossed during play
Open palm slap	On body of recipient	Open hand, palm facing recipient	C forcefully contacts P
Pinch	On skin of recipient	Thumb and one or more fingers outstretched in 'C' hand shape	C contacts P and squeezes
Poke at	On body of recipient	Finger(s) extended	C contacts P
Pull body	On body of recipient	Curved, clasping hand, or foot	C closes on P and pulls toward actor
Push body	On body of recipient	Head, feet, or hands extend toward recipient	C forcefully contacts P and pushes
Punch	On body of recipient	Hand closed into fist	C forcefully contacts P
Reach	Area between actor and recipient, oriented toward recipient	Arm or leg extended	C extended toward P and held there briefly
Sitting swagger	Area around the actor	Sitting upright	Body rocks back and forth forcefully

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