

RESEARCH ARTICLE

Differential Use of Attentional and Visual Communicative Signaling by Orangutans (*Pongo pygmaeus*) and Gorillas (*Gorilla gorilla*) in Response to the Attentional Status of a Human

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In this study we investigated the communicative abilities of 10 orangutans (*Pongo pygmaeus*) and seven western lowland gorillas (*Gorilla gorilla gorilla*), and particularly focused on their sensitivity to the attentional state of a human experimenter when choosing from a repertoire of both auditory and visual communication strategies. In experiment 1 a banana was placed in front of the subject's cage and a human experimenter was either present or absent. The subject's behavior was recorded for 60 sec. Both gorillas and orangutans gestured ($t(16) = -3.58, P < .005$) and vocalized ($t(16) = -2.47, P < .05$) more when the experimenter was present. In experiment 2 a human experimenter held a banana in front of the subject's cage and was oriented either toward or away from the subject. Again the subject's behavior was recorded for 60 sec. In this experiment both gorillas and orangutans gestured significantly more frequently ($t(16) = 3.40, P < .005$) when the experimenter was oriented toward them. In addition, gorillas and orangutans used other forms of visual communication signals, such as lip pout ($t(16) = 3.66, P < .005$), barter/trade ($t(16) = 2.31, P < .05$), and body present ($t(16) = 2.31, P < .05$) significantly more when an experimenter was facing them. The overall results indicate that both gorillas and orangutans are sensitive to the attentional state of a human experimenter and use appropriate communicative signals to gain that individual's attention. These results are also similar to previous

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INTRODUCTION

Intentional communication requires that an individual will both recognize that his behavior is informative and understand that another individual will perceive the informative nature of his behavior [Woodruff & Premack, 1979]. Moreover, for intentional communication the sender must be capable of choosing from a repertoire of appropriate signals when he attempts to communicate effectively (i.e., to change the attentional state of another). This repertoire may include both vocalizations and other forms of communication, such as facial and manual gestures. Studies of communication in nonhuman primates, particularly apes and monkeys, typically have focused on vocal communication. Fewer studies have investigated apes' abilities for gestural communication, and most of those studies focused on overall gestural repertoires rather than flexibility in gestural communication use as a form of intentional communication [Bard, 1992; Kaplan & Rogers, 2002; Fay, 1989; Fossey, 1983; Parnell & Buchanan-Smith, 2001; Pika et al., 2003; Schaller, 1963, 1964; Tanner & Byrne, 1996, 1999].

To be an effective nonverbal communicator, an individual may need to use vocal communication or other attention-getting signals as an attractor, as well as gestural forms of communication effectively in different contexts. Vocal and other auditory signals can be used to attract an individual's attention, whereas gestural communication can only be used when the recipient is already attending. The communicator will be more efficient in conveying a message if he is sensitive to this distinction. For example, when attempting to obtain a desirable object just out of reach, an individual may need to recruit the help of another individual by first vocalizing (auditory attention-getting strategy) to get the individual to orient toward them, and then gesturing (visual attention-getting strategy) to communicate with the individual about the desired object or location.

In humans, a hallmark of intentional communication in children is within-modality elaboration in communicative signaling [Lock, 2001]. Specifically, when communication fails, children will attempt to communicate again by using a different type of signal or behavior. The most efficient means of elaboration in communicative signaling is to alter the signals within a modality rather than produce a random series of communicative behaviors. These emerging abilities for recruiting another individual's attention and gesturing (such as pointing) are an important part of preverbal communication in humans [Bates, 1976; Butterworth, 2003; Lock, 2001]. Research with chimpanzees suggests that they are capable of understanding something about attentional awareness as well. For example, recent studies have demonstrated that chimpanzees gesture more frequently when a human observer is present than when the observer is absent [Call & Tomasello, 1994; Hostetter et al., 2001; Krause & Fouts, 1997; Leavens & Hopkins, 1998; Leavens et al., 1996]. This would suggest that chimpanzees understand that in order for gestural communication to be effective, an observer or recipient of the signal must be present.

Moreover, not only is the presence of another individual important, but this individual must also be attentive to the signaler. Chimpanzees appear to be sensitive to this distinction as well. Hostetter et al. [2001] found that chimpanzees

gesture more frequently and more rapidly when a human experimenter is oriented toward them than when the experimenter is oriented away from them. Similarly, Povinelli and Eddy [1996] found that chimpanzees were more likely to gesture when an experimenter was making direct eye contact with them than otherwise. Furthermore, Hostetter et al. [2001] found that chimpanzees were able to discriminate between a repertoire of effective communication strategies by choosing to vocalize more frequently and rapidly when a human experimenter was oriented away from them compared to being oriented toward them. This illustrates an understanding of not only the attentional state of the recipient of the signal, but also that one form of communication may be more effective than others given the attentional state of the observer.

In contrast to chimpanzees, little is known about sensitivity to these communicative behaviors in other apes, notably gorillas and orangutans. Studies of gestural communication in gorillas and orangutans have been limited to mostly observational studies investigating species-specific gestures as well as their overall gestural repertoire [Bard, 1992; Fay, 1989; Fossey, 1983; Kaplan & Rogers, 2002; Parnell & Buchanan-Smith, 2001; Pika et al., 2003; Schaller, 1963, 1964; Tanner & Byrne, 1996, 1999]. One limitation of such studies is that they do not specifically address how gorillas and orangutans are able to use gestural communication flexibly in combination with vocal communication given the attentional state of the recipient for the purpose of conveying information in the same way that studies have addressed this issue in chimpanzees (but see Call and Tomasello [1994]).

The present study was designed to investigate whether gorillas and orangutans use gestural and vocal communication flexibly in response to the attentional state of a human experimenter, in a manner similar to the paradigm created by Hostetter et al. [2001] in a study of chimpanzees. Their paradigm required that participants communicate with a human experimenter under more controlled settings than would be found during normal, interspecies social encounters. Although the gestures used by individuals in the present study may not be among those used during normal interaction with conspecifics (e.g., indexical pointing), this paradigm facilitated the goal of assessing the flexibility of communicative strategies used by the participants in attracting the attention of a human under controlled conditions. Our predictions were similar to those made by Hostetter et al. [2001] for chimpanzees. In experiment 1 of the current investigation, we predicted that if orangutans and gorillas are capable of understanding that their communicative signals are effective only if there is an individual present to receive them, they would attempt to communicate using gestural and vocal means more often when a human experimenter was present. In experiment 2 we predicted that if orangutans and gorillas are sensitive to the attentional states of the receiver, and that particular forms of communication are more effective given the particular attentional state of that receiver, they would use more vocal communication (attention-getting signals) when the experimenter was oriented away from the participant, and more visual signals (such as gestural forms of communication, e.g., pointing) when the experimenter was oriented toward the individual.

MATERIALS AND METHODS

Experiment 1

Subjects

The subjects were 10 orangutans (*Pongo pygmaeus*) and seven western lowland gorillas (*Gorilla gorilla gorilla*) housed at Zoo Atlanta in Atlanta, Georgia. Of the 10 orangutans (six females and four males) five were nursery-

reared, four were mother-reared, and one was wild-caught. All of the orangutans were adults and subadults (mean age = 22.8 years, SD = 10.9 years). Of the seven gorillas (two females and five males) four were mother-reared and three were wild-caught. All of the gorillas were adults and subadults (mean age = 22 years, SD = 15.5 years). American Psychological Association guidelines for the ethical treatment of animals were adhered to during all aspects of this study.

Materials and apparatus

A Sony Handycam 8 MM video recorder and a Bogen 3011 professional tripod were used to record the orangutan and gorillas' behaviors during testing. The behaviors were then coded using a JVC HR-A42U video cassette recorder and an RCA color television.

Procedure

To investigate whether the orangutans and gorillas were sensitive to the presence of a human experimenter in terms of communicative strategies, we first tested individuals in a paradigm in which an experimenter was either 1) present (i.e., standing in front of and oriented toward the individual) or 2) absent (i.e., the experimenter was not in the room with, and was therefore out of view of, the individual). This experiment was designed to test whether gorillas and orangutans would use attention-getting and visual forms of communication, such as vocalizing and gesturing, more frequently when the experimenter was present than when the experimenter was absent. The subjects were tested in the indoor, caged section of their living quarters. A camera was set up to record the individual outside their cage approximately 2 m away. A trial began after experimenter 1 walked on camera and said the subject's name and trial number. Experimenter 1 then placed a piece of banana on the ground directly in front of the subject's cage but out of reach of the individual, and walked away out of the testing area and into a separate room from the subject. After waiting exactly 60 sec (using a stopwatch), experimenter 2 walked in, announced his presence to the camera, and stood facing toward the subject so that the piece of banana was positioned on the ground between them. Experimenter 2 stood in front of the subject's cage for 60 sec. At the end of 60 sec the experimenter would give the piece of fruit to the subject regardless of its behavior and end the trial. A total of five trials were conducted for each subject in experiment 1, and the side of the cage in which the banana was placed was counterbalanced across trials for each subject.

Behavioral ethogram

Behaviors during the experimental trials were coded from the videotape using an ethogram containing 12 different behaviors: vocalization, gesture, vocalization + gesture, cage bang, lip pout, clap, spit, trade/barter, display, body present, leave/depart, d-clean, and other. These behaviors were defined previously by Hostetter et al. [2001]. *Vocalization* was recorded as any noise produced by the focal animal's mouth or throat during the trial. *Gestures* were recorded as manual gestures, such as food beg, whole hand point, or indexical point (as described by Leavens et al. [1996]). *Vocalization + gesture* was recorded as any vocalization that was produced simultaneously with a hand gesture. *Cage bang* was recorded any time one or both hands hit or pounded the cage during a trial. Any sort of manipulation of the face that involved sticking out the bottom lip was considered a *lip pout*. The coding of *clap* involved contact of one hand with the other during a trial. *Spit* was recorded any time during a trial when the individual discharged

water or saliva from its mouth toward the experimenter or the banana. Any behavior that involved the pushing of food or other items out of the cage in the direction of the experimenter and resembled sharing was recorded as a *trade/barter*. A *display* was recorded when individuals engaged in typical display behavior. If an individual offered a part of the body (e.g., back or shoulder) toward the experimenter, this was recorded as *body present*. *Leave/depart* was scored as any time the subject walked away from where the banana was lying and could no longer be seen on camera. *D-clean* indicated any displacement behavior exhibited by the gorillas that involved cleaning the cage floor or bars. *Other* was a category used to define any other behavior that was not expressly defined in the ethogram, such as poking at the banana with a stick, urinating on the banana, etc. Vocalization, cage bang and clap were considered forms of auditory attention-getting behaviors. Gestures, lip pout, spit, barter/trade, display and body present were considered visual forms of attention-getting behaviors.

In addition to recording the presence of particular behaviors, the coders also recorded the frequencies of each particular behavior. These behavioral frequencies were recorded separately for the first 60 sec of each trial when the experimenter was not present, and the last 60 sec of the trial when the experimenter was present.

Interrater reliability

The data for all 17 participants were scored by one primary coder. A second coder also scored 24% of the participants' data to assess interrater reliability. Cohen's kappa was calculated and there was a 91% agreement in behavioral categorization between observers—a value considered to be an excellent degree of reliability [Bakeman & Gottman, 1986].

RESULTS

In the initial analysis we evaluated overall differences in frequencies for gorillas and orangutans as a function of whether the experimenter was present or absent. A significant effect was found for both gesture ($t(16) = -3.58, P < .005$) and vocalization ($t(16) = -2.47, P < .05$). The gorillas and orangutans gestured and vocalized significantly more when the experimenter was present than when he was absent. In addition, there was a significant effect of lip pout ($t(16) = -2.73, P < .05$), body present ($t(16) = -2.18, P < .05$), and leave/depart ($t(16) = 2.49, P < .05$; Tables I and II). The gorillas and orangutans displayed significantly more lip pouts and body presents when the experimenter was present than when he was absent. Moreover, gorillas and orangutans left the testing area significantly more often when the experimenter was not present than when he was present. No significant differences were found between present or absent conditions for any of the other communicative behaviors, including cage bang, clap, spit, barter/trade, display, d-clean, or other. This may be due in part to their relatively low frequency of occurrence overall as compared to the other communicative behaviors. Tables I and II illustrate the frequencies and interindividual variation in communicative behaviors for gorillas and orangutans.

Species Analyses

Because of the small sample size available for testing, we did not make direct statistical comparisons between species. However, we did examine behavioral responses for the two species separately. For orangutans, a significant effect was

TABLE I. Frequencies and Inter-Individual Variation in Communicative Behaviors in Experiment 1 for Orangutans*

Behavioral category	Testing condition	
	Experimenter present	Experimenter absent
Vocalization	27 (5)	6 (2)
Gesture	26 (5)	4 (7)
Cage bang	3 (1)	2 (2)
Lip pout	19 (5)	1 (1)
Clap	2 (2)	1 (1)
Spit	4 (2)	1 (1)
Barter	12 (5)	2 (2)
Display	1 (1)	1 (1)
Leave	5 (3)	18 (7)
Other	5 (3)	4 (2)
Dclean	0	0

*Values given are number of occurrences of each behavior (number of individuals performing each behavior).

TABLE II. Frequencies and Inter-Individual Variation in Communicative Behaviors in Experiment 1 for Gorillas*

Behavioral category	Testing condition	
	Experimenter present	Experimenter absent
Vocalization	2 (2)	0
Gesture	28 (2)	6 (5)
Cage bang	2 (1)	0
Lip pout	2 (2)	0
Clap	0	0
Spit	0	0
Barter	0	0
Display	3 (1)	1 (1)
Leave	0	4 (2)
Other	0	0
Dclean	18 (2)	10 (3)

*Values given are number of occurrences of each behavior (number of individuals performing each behavior).

found for vocalization ($t(9) = -2.44, P < .05$), gesture ($t(9) = -3.16, P < .05$), and lip pout ($t(9) = -2.71, P < .05$; Table I). The orangutans produced significantly more vocalizations, gestures, and lip pouts when the experimenter was present than when he was absent. For gorillas, a trend was found for gesture ($t(6) = -2.09, P < .10$) and body present ($t(6) = -2.29, P < .075$). The gorillas tended to gesture and present body parts more frequently when the experimenter was present vs. absent. The marginal results may be due in part to the relatively small number of gorilla subjects.

Latency for First Behavior Responses

We also analyzed the latency to perform first behavior responses to evaluate whether these latencies for behaviors differed as a result of condition (experimenter present vs. absent). We measured the time in seconds that it took for an individual

to produce a first behavior response in each trial and compared these responses between conditions. If an individual performed a behavior in one condition but not in the other, the individual received a latency score of 60 sec for the condition in which the behavior was not elicited. If an individual did not perform a particular behavior in either condition, this behavior was not included in the analysis.

For orangutans, we found a significant difference in latency when the experimenter was present compared to when he was absent in terms of vocalizations ($t(8) = 2.28, P < .05$), gesturing ($t(8) = 8.38, P < .001$), lip pout ($t(8) = 5.82, P < .005$), and leaving ($t(8) = -3.79, P < .005$). For gorillas, we found a significant difference in latency between the two conditions for gesturing ($t(6) = 8.37, P < .001$), lip pout ($t(6) = 7.44, P = .005$), and leaving ($t(6) = -13.03, P < .01$). As expected, individuals were quicker to gesture and lip pout (and vocalize, for orangutans) when the experimenter was present to receive this signal. When no experimenter was present to receive a signal, individuals were quicker to walk away or leave the testing area.

DISCUSSION

The results from experiment 1 indicate that orangutans and gorillas are sensitive to the presence of a human experimenter in terms of their communicative behaviors. In other words, gorillas and orangutans use different forms of communication depending on the attentional state of the human experimenter. The overall results for both species indicate that they vocalize and gesture more when a human experimenter is present than when he is absent. In addition, they produce more attention-getting behaviors, such as lip pout and body present, in the presence of an experimenter. We also found that the gorillas and orangutans tended to leave the testing area more frequently when no human experimenter was present. Taken together, these results suggest that gorillas and orangutans are sensitive to the communicative nature of their behavior. Furthermore, these findings suggest that gorillas and orangutans use signals intentionally to attract the attention of the human experimenter. This sensitivity on the part of these apes appears to fulfill the criteria proposed by Woodruff and Premack [1979] to define intentional communication (i.e., communication is intentional if an individual recognizes that his behavior is informative and understands that another individual will perceive the informative nature of his behavior).

Next we attempted to address whether gorillas and orangutans could choose from a repertoire of communicative behaviors depending on which would be most effective given the attentional state of the recipient. Therefore, experiment 2 was designed to investigate whether gorillas and orangutans would alter the communicative signals they produce based on whether the human experimenter was attending to them directly or not (i.e., facing toward them and looking at them vs. facing away from them and not looking at them).

Experiment 2

Subjects and apparatus

The subjects and recording equipment used in experiment 2 were the same as those used in experiment 1.

Procedure

To investigate whether the gorillas and orangutans would alter their communicative strategies based on the attentional state of the human

experimenter, we tested individuals in a paradigm similar to that used for chimpanzees by Hostetter et al. [2001]. This paradigm involves two conditions: 1) the experimenter is oriented toward the subject, and 2) the experimenter is oriented away from the subject. A camera was set up about 2 m away from the subject's cage and recorded all behaviors during each 60-sec trial. In condition 1, a human experimenter approached the subject's cage and announced the subject's name, condition, and trial number. He then crouched down in front of the subject about 1 m away from the cage, holding half of a banana. The experimenter held the banana in front of him and looked directly at the subject, and thus the subject could see the banana and the human experimenter's face. Using a stopwatch to time the trial, the experimenter would remain in front of the subject for 60 sec. At the end of 60 sec the experimenter would give the banana to the subject regardless of the individual's behavior. Condition 2 involved the same sequence of events; however, when the experimenter crouched in front of the subject, he faced away from the individual and held the banana behind his back. Thus, the subject could see the banana but could not see the human experimenter's face. Each trial in condition 2 lasted 60 sec. At the end of the 60 sec, the experimenter would give the banana to the subject regardless of the individual's behavior. Each subject participated in five trials in each condition, and the conditions were counterbalanced across subjects. The same behavioral ethogram use in experiment 1 was employed here. Latency to onset of the first communicative behavior was also recorded in this experiment following the same procedure described previously.

RESULTS

We first analyzed overall differences between conditions for gorillas and orangutans using paired *t*-tests. We found a significant effect of gesture ($t(16) = 3.40$, $P < .005$), but not for vocalization. In other words, gorillas and orangutans gestured significantly more frequently when the human experimenter was oriented toward the subject (i.e., the subject could see the experimenter's face) than when he was oriented away from the subject. This was not the case, however, for vocalizations. There was no significant difference in the amount of vocalizing between the toward and away conditions. In addition, we found a significant effect for lip pout ($t(16) = 3.66$, $P < .005$), barter/trade ($t(16) = 2.31$, $P < .05$), body present ($t(16) = 2.31$, $P < .05$), and leave/depart ($t(16) = -2.31$, $P < .05$). The gorillas and orangutans would lip pout, barter/trade, and present parts of the body significantly more frequently when a human experimenter was oriented toward them vs. oriented away from them. Conversely, the gorillas and orangutans left the testing area significantly more when the human experimenter was oriented away than when he was oriented toward them. There was no significant effect of any other recorded communicative behavior, including clapping, spitting, displaying, d-cleaning, or other. Tables III and IV illustrate the frequencies and interindividual variation in communicative behaviors for gorillas and orangutans.

Species Analyses

We also analyzed orangutans and gorillas separately to investigate trends in behavioral differences for the two species. For orangutans there was a trend toward increased use of gestures ($t(9) = 2.10$, $P = .065$). Orangutans tended to gesture more when the experimenter was oriented toward them than when he was oriented away from them. There was a significant effect of lip pout for

TABLE III. Frequencies and Inter-Individual Variation in Communicative Behaviors in Experiment 2 for Orangutans*

Behavioral category	Testing condition	
	Toward	Away
Vocalization	10 (3)	13 (4)
Gesture	47 (6)	1 (1)
Vocalization and gesture	0	0
Cage bang	3 (1)	9 (3)
Lip pout	57 (8)	8 (5)
Clap	1 (1)	0
Spit	6 (3)	21 (2)
Barter	40 (8)	25 (5)
Display	2 (1)	0
Leave	9 (3)	15 (5)
Other	5 (4)	5 (4)
Dclean	0	0

*Values given are number of occurrences of each behavior (number of individuals performing each behavior).

TABLE IV. Frequencies and Inter-Individual Variation in Communicative Behaviors in Experiment 2 for Gorillas*

Behavioral category	Testing condition	
	Toward	Away
Vocalization	11 (3)	2 (2)
Gesture	89 (7)	22 (3)
Vocalization and gesture	1 (1)	1 (1)
Cage bang	23 (4)	30 (3)
Lip pout	13 (3)	0
Clap	0	0
Spit	0	0
Barter	9 (3)	6 (2)
Display	5 (1)	1 (1)
Leave	11 (4)	14 (4)
Other	1 (1)	5 (1)
Dclean	49 (4)	25 (4)

*Values given are number of occurrences of each behavior (number of individuals performing each behavior).

orangutans ($t(9) = 3.52$, $P < .05$). The orangutans lip-pouted significantly more when the experimenter was facing toward them. In addition, there was a marginal effect of barter/trade ($t(9) = 2.18$, $P = .057$). The orangutans tended to attempt to barter/trade with the experimenter more frequently when he was oriented toward them. No significant effects were found for any other communicative behaviors, including vocalization, cage banging, clapping, spitting, displaying, body presenting, leaving, or other. For gorillas there was a significant effect for gesturing ($t(6) = 2.76$, $P < .05$). The gorillas gestured significantly more when the experimenter was faced toward them. No other significant effects were found for any other communicative behaviors on the part of the gorillas.

Modality Effects

Rather than focus on each individual communicative behavior, we compared more broadly the function of the communicative signaling in relation to the orientation of the human. For this analysis we classified the communicative behaviors as visual or auditory/attention-getting behaviors. For the visual category we averaged the total frequency of gestures, lip pouts, barters, and presents in the toward and away conditions. For the auditory category we averaged the total frequency of vocalizations, claps, spits, and cage bangs for the toward and away conditions. The averages in each condition were compared between species using a mixed model analysis of variance (ANOVA). Condition (away, toward) and modality (visual, auditory/attentional) were repeated measures, and species was the between-group variable. A significant two-way interaction between modality and condition was found ($F(1, 15) = 21.53, P < .001$). Post-hoc Tukey's HSD analysis indicated that the apes used more visual signals than auditory/attentional signals when the human was facing toward them compared to away from them. The mean numbers of communicative behaviors in each condition and modality with standard errors are shown in Fig. 1. These results were consistent between gorillas and orangutans.

Elaboration in Signaling

Another hallmark of intentional communication in children is within-modality elaboration in communicative signaling [Lock, 2001]. Specifically, when communication fails, children will attempt to communicate again by using a different type of signal or behavior. The most efficient means of elaboration in communicative signaling would be to alter the signals within a modality rather than produce a random series of communicative behaviors. To evaluate whether the apes elaborated their communicative behaviors, we calculated the total number of different communicative behaviors they produced that were either visual or auditory/attentional in each condition. These data were subjected to a mixed model ANOVA with condition (away, toward) and modality (visual, auditory/attentional) serving as repeated measures, while species was the between-group variable.

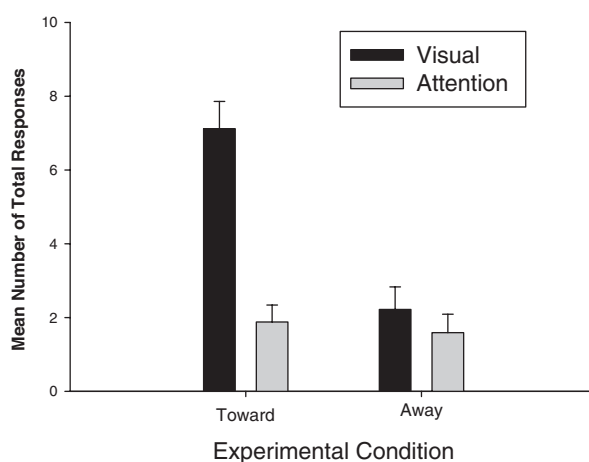


Fig. 1. Mean number of visual and attentional behaviors as a function of whether the human was facing toward or away from the focal subject.

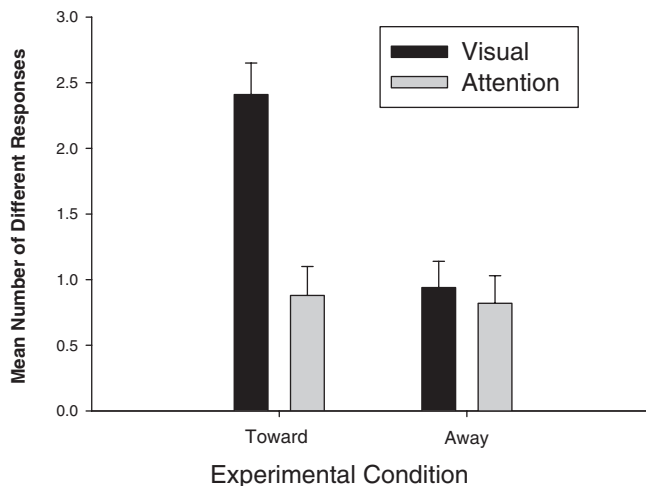


Fig. 2. Mean number of different visual and attentional communicative behaviors produced as a function of whether the human was facing toward or away from the focal subject.

We found a significant interaction between condition and modality ($F(1, 15) = 25.05, P < .001$; Fig. 2). Post-hoc analysis indicated that the apes elaborated their visual signals more when the human was facing them compared to when the human was facing away. In contrast, the apes did not significantly elaborate their auditory communicative signals depending on the orientation of the human.

Latency for First Behavior Responses

Finally, we analyzed the latency to perform first behavior responses to see whether these latencies for behaviors differed as a result of the orientation of the experimenter (toward vs. away). We measured the time in seconds that it took for an individual to produce a first behavior response in each trial, and compared these responses between conditions. If an individual performed a behavior in one condition but not in the other, the individual received a latency score of 60 sec for the condition in which the behavior was not elicited. If an individual did not perform a particular behavior in either condition, this behavior was not included in the analysis.

For orangutans we found a significant difference in latency between the two conditions for cage banging ($t(8) = 56.31, P = .011$) and lip pouting ($t(8) = -5.00, P < .001$). For gorillas we found a significant difference in latency between the two conditions for gesturing ($t(6) = -2.77, P = .01$), lip pouting ($t(6) = -32.86, P = .001$), cage banging ($t(6) = 10.95, P = .000$), and leaving ($t(6) = 4.50, P = .01$).

DISCUSSION

The results of experiment 2 indicate that gorillas and orangutans appear to be sensitive to the attentional state of the human experimenter. Overall, the apes used visual communication signals significantly more frequently when an experimenter was oriented toward them. In other words, the apes appeared to be sensitive to the fact that gestural communication is more effective if an individual is oriented toward them and attending to them. In contrast, when the human was facing away, the apes used more attention-getting behaviors such as vocalizing, clapping, cage banging, or spitting. These results support the view that gorillas and orangutans are sensitive to the use of visual signals (e.g., gestures, lip

pouts, barters, and body presents) if the human is oriented toward them/visually attending. In addition, they appear to be sensitive to the use of auditory or attention-getting behaviors (e.g., cage bangs) to recruit the attention of another individual. These results are very similar to those obtained in previous studies with chimpanzees [Hostetter et al., 2001; Leavens et al., 2004]. One difference between this study and previous studies with chimpanzees is the greater number of trials conducted in the current investigation. A greater number of trials were utilized to compensate for the smaller sample size available. As a result, a potential confound of the current investigation is learning effects on the part of the subjects. It is possible that the subjects learned they would be given the reward at the end of the 1-min trial regardless of behavior. Table V illustrates the number of subjects that gestured as a function of condition in each trial. These results suggest that learning effects did not influence visual communication. The table illustrates that the number of gesturing individuals did not vary across trials (in particular, compare trials 1 and 5).

Furthermore, the results indicate species-specific differences in the types of visual signals preferred most by the gorillas and orangutans. When we analyzed types of visual communication for each species, we found that the orangutans used significantly more lip pout in the toward condition compared to the away condition, whereas for the gorillas we found significantly more manual gestures in the toward condition compared to the away condition. The orangutans used significantly more lip pouts when the experimenter was oriented toward them, while the gorillas apparently preferred using manual gestures more to communicate with the experimenter. The extent to which these species differences in types of visual communicative signals generalize to the species as a whole outside of the context of the Zoo Atlanta populations remains to be determined. Our observations, however, are consistent with at least one other experimental report on communication in orangutans and gorillas. Liebal et al. [in press] similarly found that orangutans were more prone to use lip-pouts as a form of visual communication with a human experimenter, whereas gorillas were more likely to use manual gestures (as were chimpanzees and bonobos). It is not known whether gorillas and orangutans use these same communicative behaviors as visual signals when attempting to communicate with members of their own species, or whether these behaviors are specific to their interactions with humans. These questions merit further investigation.

Interestingly, elaboration in signaling behavior was restricted to the visual domain in the toward condition. The apes produced significantly more and different visual signals when the human was facing toward vs. away from them.

TABLE V. Number of Individuals Gesturing as a Function of Condition*

	Trial number				
	1	2	3	4	5
Experiment 1					
No experimenter	1	1	2	3	1
Experimenter	8	7	7	6	7
Experiment 2					
Experimenter toward	1	3	2	4	2
Experimenter away	9	8	10	12	8

*Total number of individuals = 16.

In contrast, the apes did not produce different types of auditory attention-getting signals depending on the orientation of the human. Thus, elaboration in signaling appears to be limited to the visual modality in orangutans and gorillas. This result differs from recent findings in chimpanzees. Hopkins et al. (unpublished results) found that chimpanzees produce modality-specific elaboration in their signaling depending on whether a human holding food is facing toward or away from them. Why chimpanzees differ from other apes is unclear, but discrepancies in sample size may be one important factor. Whereas the study by Hopkins et al. included 110 subjects, the present study involved a relatively small sample. Additional studies on elaboration in communicative signaling may prove important for understanding the intentionality of ape communicative abilities.

CONCLUSIONS

The results of these studies illustrate that gorillas and orangutans, like chimpanzees, are sensitive to the presence of an audience and are capable of producing intentional communicative behaviors in an attempt to recruit the attention of that audience. In addition, these studies suggest a propensity by gorillas and orangutans to control the types of communicative behaviors used depending on the attentional state of the audience. Although these results are similar to previous findings in chimpanzees, we do see that there are species-specific differences in the types of attention-getting communicative behaviors displayed. For example, chimpanzees tend to use a wide range of attention-getting behaviors, such as cage banging, spitting, clapping, and vocalizations, when an audience is oriented away from them [Hostetter et al., 2001; Leavens et al., 2004]. Although orangutans and gorillas tend to cage bang more quickly when the audience is oriented away from them, the data from the current investigation suggest that leaving the testing area is a viable alternative for these individuals. These behaviors demonstrate a sensitivity to the orientation of the audience while they exemplify a difference in strategies for recruiting that attention. In other words, while it seems to be the case that all three species adjust their behaviors based on the attentional state of the human, they employ different means of attempting to manipulate that attention for the purpose of engaging the audience in joint attention about something in the environment. All three species exhibit a flexibility in their communicative behavior, which is an indicator of intentional communication.

We also observed similar species differences in communicative behaviors in terms of visual attention-getting strategies. These visual attention-getting strategies are those used within the context of a social partner that is oriented toward the communicator. This is in contrast to attention-getting strategies, as described above, which require the individual to first recruit the attention of another individual that is not oriented toward the attention seeker. More than likely, these attention-getting strategies require an auditory component to orient the individual's attention in the communicator's direction. Once the individual is oriented toward the attention seeker by means of auditory communicative behavior, the latter can employ visual behaviors to further engage the attention of that individual about the object or situation in question. Like chimpanzees [Hostetter et al., 2001], orangutans use significantly more lip pouts when an experimenter is oriented toward them vs. away from them. However, we found only a marginal effect of gesture and barter/trade used by orangutans as a visual communicative behavior. Gorillas, on the other hand, used significantly more gestures as a visual means of gaining the experimenter's attention when he was

oriented toward them vs. away from them. This apparently was the gorillas' primary means of communicating visually about the food item in the current investigation, since we found no effect for any other type of visual communicative behavior. In comparison with previous findings in chimpanzees [Hostetter et al., 2001], the current results in gorillas and orangutans suggest that chimpanzees use more attention-getting behavior in more appropriate contexts; however, these differences may reflect the large sample size of chimpanzees available for testing in the previous study. More individual variability was found for chimpanzees in terms of communicative abilities. Due to the limited number of gorillas and orangutans available for testing in the present study, it is difficult to conclude whether similar trends exist in these species as well. As a result, we have less power to draw comparisons between the species tested here and previous investigations with chimpanzees.

Orangutans and gorillas did not use auditory attention-getting behaviors (including vocalizations) to capture the attention of an otherwise inattentive human, based on the findings in experiment 2. These findings are consistent with previous studies in captive chimpanzees [Theall & Povinelli, 1999] but not with other findings [Hostetter et al., 2001; Leavens et al., 2004]. The discrepancy in results among studies of captive chimpanzees, as well as great ape species, may be related to sample size. In the studies by Hostetter et al. [2001] and Leavens et al. [2004], relatively large samples of subjects were used, in contrast to the studies by Theall and Povinelli [1999] and this study. There is considerable individual variation in the use of attention-getting behaviors and vocalizations by captive chimpanzees, and larger sample sizes are needed to detect any differences between experimental conditions. Until larger cohorts of orangutans and gorillas are tested, the question of how they functionally use attention-getting behavior and vocalizations remains an open issue.

The collective results indicate that not only are gorillas and orangutans (like chimpanzees) capable of modifying their communicative behavior based on the presence or absence and the attentional state of a communicative partner, they also appear to show between-species differences in how they modify this behavior and what types of visual and auditory attention-getting communicative behaviors they prefer to use. This suggests that apes are capable of communicating intentionally as described by Woodruff and Premack [1979] and can use different communicative behaviors flexibly and appropriately given the attentional state of their audience. We know that these flexible communicative abilities are an important part of intentional communication for preverbal human infants [Butterworth, 2003; Lock, 2001]. The current investigation reinforces the view that humans are not the only species capable of such sensitivity when recruiting and engaging attention about an object in the environment from another individual. These results further suggest that apes (more specifically gorillas and orangutans) do not simply use behaviors such as gestures and vocalizations as a reaction to stimuli in their environment; rather, they understand something about the communicative nature of these behaviors and can use them to manipulate a social agent to obtain an otherwise unobtainable food item. Moreover, these ape species are capable of discriminating between a repertoire of behaviors in order to choose the most appropriate and effective behaviors for recruiting and directing another's attention about items or events in the environment. The extent to which these findings in captive ape species would generalize to wild populations is unknown; however, the existence of these abilities under controlled experimental conditions suggests that apes have a capacity for intentional communication similar to that found in humans. Further

studies are needed to determine whether these species-specific differences in intentionally communicative behaviors are consistent over larger populations in various settings.

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