To move or not to move

How apes adjust to the attentional state of others[*]

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A previous observational study suggested that when faced with a partner
with its back turned, chimpanzees tend to move around to the front of a
non-attending partner and then gesture — rather than gesturing once to
attract attention and then again to convey a specific intent. We investigated
this preference experimentally by presenting six orangutans, five gorillas,
nine chimpanzees, and four bonobos with a food begging situation in which
we varied the body orientation of an experimenter (E) with respect to the
subject (front vs. back) and the location of the food (in front or behind E).
These manipulations allowed us to measure whether subjects preferred to
move around to face E or to use signals to attract her attention before they
begged for food. Results showed that all species moved around to face E and
then produced visual gestures, instead of using tactile/ auditory gestures
behind E to call her attention. Species differences were apparent particularly
when the food and E were in different locations. Unlike gorillas and orang-
utans, chimpanzees and bonobos (from genus *Pan*) produced their gestures
in front of E in all conditions, including that in which subjects had to leave
the food behind to communicate with her. Implications of these results are
discussed in the context of the evolution of social cognition in great apes.

Keywords: Great apes, evolution, social cognition, gesture

Introduction

Communication is sometimes defined so broadly that it includes all forms of
information transfer between individuals, including cases in which one individual

makes inferences about another (unknowing) individual based on its behavior. But defined more narrowly communication requires that one individual (a sender) does something in order that another does something (a receiver). The term intentional communication has sometimes been used to identify this special case.

Nonhuman primates engage in intentional communication in the sense that senders direct signals to receivers and have specific goals for doing so; for example, they want the other to play, or groom, or allow nursing, or give food, or go away, and so forth (Tomasello et al., 1985). As for all goal-directed behavior, the goal is inferred from the sender's signs of dissatisfaction when the other does not do what he wants it to (including making further attempts) and signs of satisfaction (including a cessation of attempts) when the goal has been met (Bruner, 1973). The interesting cognitive question in all of this is how senders understand the way their signals function — through the recipient — to help them achieve their goals. Specifically, we may ask whether senders understand that recipients must perceptually attend to their signals if effective communication is to take place.

Tomasello et al. (1985, 1989, 1994, 1997) identified around three dozen gestures that young chimpanzees use to communicate with group mates in various contexts. For instance, they raise their arms to initiate play, extend their arm to beg for food, slap the ground or clap their hands to call attention to themselves, and touch their mother's side to request traveling to a different location. These gestures fall within three basic sensory modalities: visual, auditory, and tactile. Thus, visual gestures rely solely on visual information (e.g., hand-beg), auditory gestures rely mainly on sound production (e.g., hand-clap), and tactile gestures depend mainly on establishing physical contact with the recipient (e.g., arm on). Tomasello et al. (1994, 1997) found that chimpanzees use gestures from the three sensory modalities differentially depending on the spatial orientation of the recipient. In particular, young chimpanzees use gestures that are mainly auditory or tactile when their recipient was in all kinds of spatial orientations with respect to them, but they use visual gestures only when their recipient is facing toward them and therefore able to see them. One possible conclusion from these data is that chimpanzees know that if their visually based gestures are to work, others must see them.

Experimentally, this is supported by Leavens et al. (2004) who found that chimpanzees adjust their communicative behavior according to the attentional orientation of a human experimenter. Depending on condition, the human experimenter offered food either to the focal subject or to another chimpanzee

in the same or adjacent cage. The behavioral sequences of the focal subject to beg for the food were unimodal (visual-visual) or bimodal (visual — vocalization), respectively, if the human's attention was directed towards themselves, but changed to auditory-auditory sequences if the human's attention was focused at another chimpanzee.

Call and Tomasello (1994) investigated begging behaviors (including gestures such as poke, knock, lip begging) of two orangutans (*Pongo pygmaeus)* to obtain food from a human experimenter who in different experimental conditions either stared at the individual with the eyes open, stared at the individual with the eyes closed, sat with the back towards the individual or left the room. Results showed that orangutans gestured more often when the experimenter was oriented to them, and one of the orangutans also responded more often when the experimenter's eyes were open rather than closed. Hostetter et al. (2001) examined the use of vocalizations and manual gestures of 49 chimpanzees as a means of gaining the attention of a human experimenter. The chimpanzees were tested in three conditions: (i) the experimenter turned his back but held a banana behind his back, (ii) the experimenter looked directly at the subject while holding a banana in front of him, and (iii) the experimenter placed a banana in front of the chimpanzee's cage and left the testing area. Results showed that chimpanzees uttered vocalizations faster and were more likely to produce vocalizations as their first communicative behavior in the oriented-away condition (manual gestures were used more frequently and faster in the oriented-toward condition), presumably as a way to get the human's attention. In contrast to these positive findings, Povinelli and Eddy (1996; see also Theall & Povinelli, 1999) found that although chimpanzees gestured preferentially to humans whose body was oriented toward them rather than away from them (thus confirming previous findings), in certain more complex situations chimpanzees did not seem to show sensitivity to the attentional state of the human. For instance, when the human simply faced the chimpanzee but closed her eyes (or placed a bucket on her head), chimpanzees gestured anyway; when she turned her back but looked over her shoulder at the chimpanzees, they did not gesture.

However, Kaminski et al. (in press) argued that the study of Povinelli and Eddy (1996) confounded two factors: the human's bodily orientation, which indicates her ability to obtain and give the chimpanzee the food, and perceptual orientation, which indicates her ability to perceive the signal. They tested chimpanzees, bonobos, and orangutans in two different experiments. In the first experiment, they found, that all of the apes gestured preferentially when the

experimenter was oriented toward them facially and bodily as it was found in previous studies. In the second experiment, however, the experimenter's body and face orientation were systematically manipulated so that the human could have her body and/or face oriented either towards or away from the tested individual. Contrary to the findings of Theall and Povinelli (1999), the results of this experiment showed that all three ape species were sensitive to the body and face orientation of the experimenter separately (see also Gomez, 1996). Specifically, apes gestured more to the human when her face was oriented toward them than when it was oriented away, but only if her body was in a position to deliver the food. Kaminski et al. therefore concluded that body and face orientation signal two different types of information: face orientation indicates the human's perceptual access to the signal, whereas body orientation indicates the human's ability and disposition to provide food.

Povinelli et al. (2001) showed that chimpanzees alter the location where they produce their visual gestures depending on whether the attention of a human experimenter was focused at the food they desired, at a distracter-object, or at the ceiling. Accordingly, the chimpanzees modified their patterns of gesturing to compensate for a mismatch between the object they wanted (food) and the attentional focus of the human.

Although individuals in these studies were sensitive to the attentional state of humans and deployed their gestures accordingly, we found little evidence in our previous studies suggesting that chimpanzees also attempt to manipulate the attentional state of a non-attending recipient to get him to attend — so that they could then provide a more specific signal (e.g., begging). In an attempt to investigate this possibility, we conducted systematic observations of chimpanzee gesture sequences to determine whether chimpanzees would call the attention of a non-attending recipient before using visual gestures (Liebal et al., in review). Contrary to our expectations we found little evidence of active manipulation of attentional states. But we observed something else quite intriguing. Chimpanzees tended to move into the attentional field of the recipient by walking in front of him and then performed visual gestures. Thus, these data suggested that before gesturing to a non-attending recipient, chimpanzees preferred to move around themselves to face the recipient rather than making the recipient move to face them. The aim of the current study was to see if we could reproduce the use of this strategy under experimental conditions. Therefore, we presented a situation in which apes could beg food from a non-attending human, but unlike previous studies they were given the option to either (1) move around the experimenter and then gesture or (2) call attention

and then gesture. All four great ape species (chimpanzees, bonobos, gorillas, orangutans) were tested under identical conditions, thus giving us the possibility of testing different possible phylogenetic hypotheses about the origin of skills of gestural communication and social cognition.

Methods

Subjects

Six orangutans (*Pongo pygmaeus*), five gorillas (*Gorilla gorilla*), nine chimpanzees (*Pan troglodytes*) and four bonobos (*Pan paniscus*) participated in this experiment (Table 1). There were eight males and 16 females ranging from 5 to 30 years of age. 10 apes were hand reared and 12 were reared by their mothers. For two individuals the rearing history is unknown. All apes were housed at the Wolfgang Köhler Primate Research Center at Zoo Leipzig (Germany). They lived in social groups with conspecifics and had access to indoor and outdoor areas. During testing, the apes were fed according to their daily routine four times a day on a diet of fruit, vegetables and monkey chow; water was available ad libitum.

Experimental setup

Testing took place in the indoor area. Figure 1 shows the ground view of the experimental setup. The testing cage consisted of two sections separated by a door, which was opened during testing. The experimental booth consisted of the area next to the sides 1 to 3. The human experimenter (E) sat on a chair facing the ape at the beginning of each trial. Side 1 and 3 of the cage consisted of Plexiglas panels with three holes in it, which were large enough that the apes could reach through with their fingers. Side 2 was covered with cardboard to block the view of the subject and therefore avoid interactions with E at this side. Two video cameras were placed at two different locations to record the subject's behavior. A stopwatch was used to measure the time and a clipboard served to make notes between test trials. Based on individual's preference different food items (banana, grapes, etc.) were offered as rewards. The food was in a bowl (B), which E either held in her hands in front of her or placed behind her depending on the condition.

Table 1. Subjects who participated in the study. For each individual, its name, sex, date of birth and rearing history are shown.

Species	Individual	Sex	Date of birth	Rearing history
Bonobo	Joey	Male	1982–12–13	Hand reared
	Kuno	Male	1996–11–26	Hand reared
	Limbuko	Male	1995–10–04	Hand reared
	Ulindi	Female	1993–10–10	Mother reared
Chimpanzee	Dorien	Female	1980–10–22	Hand reared
	Fifi	Female	1993–05–12	Mother reared
	Fraukje	Female	1976–04–06	Hand reared
	Gertrudia	Female	1993–05–20	Mother reared
	Jahaga	Female	1993–01–06	Mother reared
	Riet	Female	1977–11–11	Hand reared
	Robert	Male	1975–12–01	Hand reared
	Sandra	Female	1993–06–06	Mother reared
	Ulla	Female	1977–06–08	Hand reared
Gorilla	Bebe	Female	1979–00–00	Unknown
	Gorgo	Male	1981–06–28	Hand reared
	N'diki	Female	0000–00–00	Mother reared
	N'kwango	Male	1996–09–22	Mother reared
	Ruby	Female	1997–12–19	Hand reared
Orangutan	Bimbo	Male	1980–09–20	Unknown
	Dunja	Female	1973–04–19	Mother reared
	Padana	Female	1997–11–18	Mother reared
	Pini	Female	1988–06–30	Mother reared
	Toba	Female	1994–02–07	Mother reared
	Walter	Male	1989–04–24	Mother reared

Procedure

One experimenter (second author) tested the gorillas and chimpanzees, while a second experimenter (first author) tested the bonobos and orangutans. The apes received no special training. All of them were used to enter the testing area and to beg for food because of their prior participation in other experiments. In an initial period preceding each trial the experimenter gave the subject several pieces of food. After 10 s elapsed and the subject was facing the experimenter, a test trial began consisting of one of the following four conditions:

E stays with B: Experimenter waits with the bowl in her hands facing the subject (see Figure 1). This condition was designed to investigate which behaviors the different species use to beg for food from the experimenter.
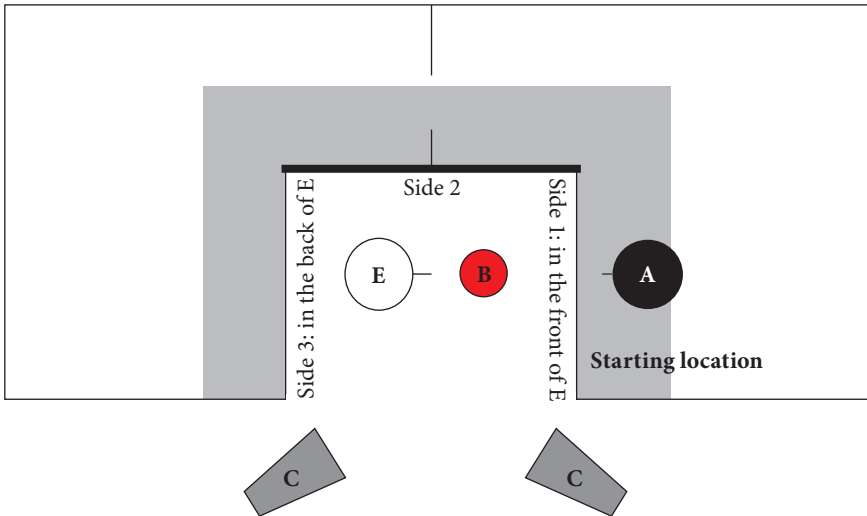
Figure 1. Experimental set up (ground view) of the *E stays with B* condition and of each initial period preceding the other conditions. The experimenter (E) is sitting in front of the ape (A) with a bowl with food (B) in her hands. Dashes indicate E's and the subject's facial orientation. Side 1 and side 3 represent the two target locations (in front of E, in back of E); side 2 is covered with cardboard. The area marked in grey indicates the experimental booth. Two cameras (C) are placed to record the apes behavior at side 1 and 3, respectively.

E moves with B: Experimenter turns at 180° with the bowl in her hands (Figure 2a). This condition was designed to test whether apes would move around to face the experimenter and then produce visual gestures instead of staying behind the experimenter to use tactile or auditory signals serving to attract the recipient's attention.

E stays, B moves (control 1): Experimenter is still facing the subject, but places bowl behind her (Figure 2b). This control condition evaluated the effect of moving the bowl only to the alternative location.

E moves, B stays (control 2): Experimenter places the bowl in front of her and then moves at 180° (Figure 2c). This condition evaluated the effect of moving the experimenter only to the alternative location.

Each trial lasted 20s. After this time elapsed the subject always received a piece of food independent of its performance. Each subject took part in two sessions (=24 trials), each consisting of 3 blocks of 4 trials (conditions 1 to 4) with the order of conditions randomized across subjects. Subjects participated in only
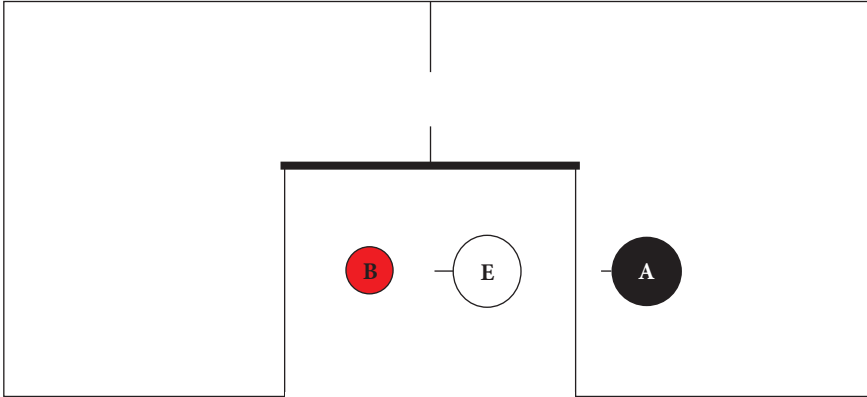
Figure 2a. *E moves with B* condition: E turns 180º together with B.

one session per day. The number of trials starting from side 1 and side 3, respectively, was counterbalanced to control for a side bias. We expected that subjects would not move in the conditions where E stayed (*E stays with B; E stays, B moves*), but would move in case E moves (*E moves with B; E moves, B stays*).
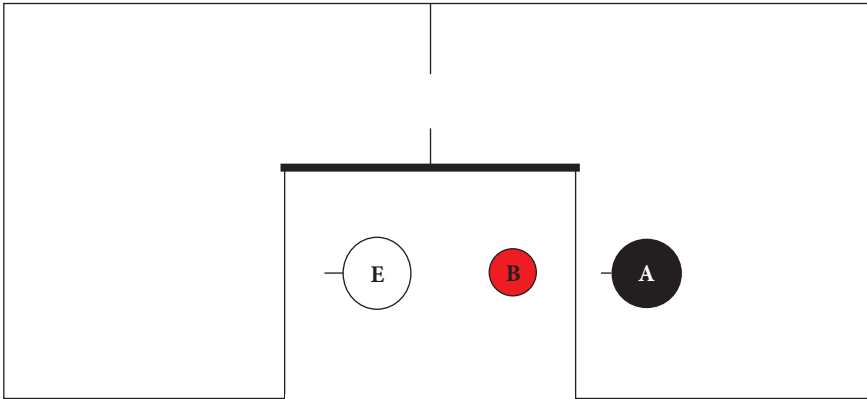
Data analysis

All trials were videotaped and later coded by one of the experimenters (first author). We used two main dependent measures to assess the subjects' responses to the experimental manipulations. One dependent measure consisted of the
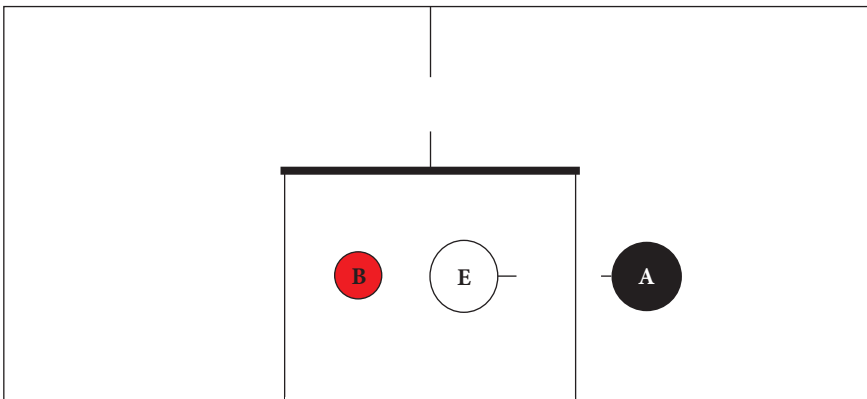
Figure 2b. *E stays, B moves* condition (control 1): E stays and faces the ape, but places B behind her.

Figure 2c. *E moves, B stays* condition (control 2): E turns around, but B remains behind her.

percentage of trials in which the subject moved from side 1 (i.e., the ape's initial starting location at the beginning of the trial) to side 3. We defined two different target locations: in front of E and in the back of E. The other dependent measure was based on the apes' signal production. We distinguished three major signal categories: visual, tactile, and auditory. Visual signals consisted of behavioral displays involving no physical contact or producing no auditory information. These included expressive movements of limbs or head and body postures and facial expressions. Tactile signals consisted of expressive movements of limbs involving physical contact with the experimenter. Finally, auditory signals consisted of either expressive movements of limbs or head generating non-vocal sounds and vocalizations. We coded whether each signal was performed in front or behind the experimenter as well as the total frequency of each signal category per trial. We calculated the mean frequency of signals per subject and the individual's mean percentage of signals performed in front and behind the experimenter for each signal category.

Since chimpanzees and bonobos showed a similar behavior with respect to the percentage of movements and use of signals in the different conditions, data of both species were pooled for subsequent data analysis on genus level (*Pan, Gorilla, Pongo*). The different rearing histories of the subjects had no effect on their movements as well as their use of signals. Therefore, data of mother- and hand-reared subjects were combined. To assess reliability, 20 % of the data were coded by a second person unaware of the task of this study. Cohen's kappa was used to measure the degree of the concordance for movements and signals

which was 0.86 and 0.82, respectively ('very good' level of agreement, Altman, 1991). An ANOVA (repeated measurements) was applied to analyze the effect of several independent variables on the percentage of movements and use of signals.

Results

Results will be presented first for apes' movements and second for their used signals under different conditions in the experiment.

Movements

Figure 3 shows for each genus the mean percentage of trials in which subjects moved to the alternative location (180° from their starting point) depending on condition. For this analysis we only considered the first movement a subject performed in the trial. A 4×3 ANOVA with condition as within-subject factor and genus as between-subject factor on the percentage of movements indicated a significant effect for condition, $F(3,63)=31.47$, $p<0.001$, and no effect for genus, $F(2,21)=1.19$, $p=0.33$, or condition × genus, $F(6,63)=2.05$, $p=0.073$.

A post hoc pairwise comparison showed that subjects moved significantly more often in the *E moves with B* condition compared to all other conditions
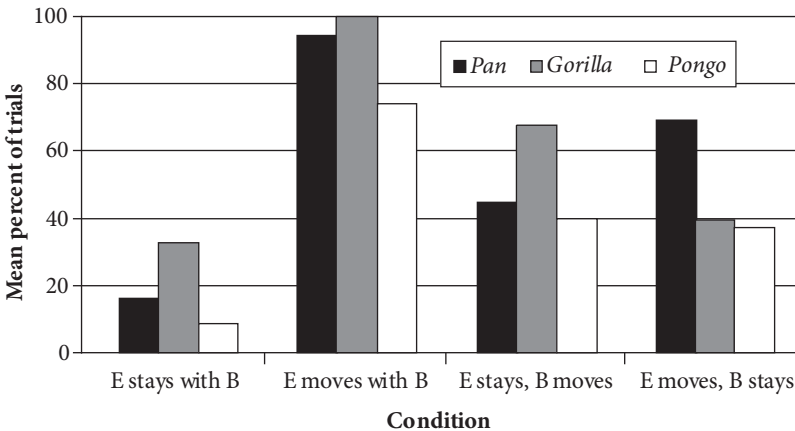

Figure 3. Mean percent of trials in which subjects moved to the alternative location depending on condition and shown for each genus (only the first movement between target locations is considered).

(p < 0.001), while they moved least in the *E stays with B* condition compared to all other conditions (p = 0.001). This means that subjects moved more often when the experimenter and the bowl moved. However, this analysis does not clarify the reason for the movement: the experimenter or the bowl. An analysis of the two control conditions in which only one of the elements moved can answer this question. Thus, we conducted a 2×3 ANOVA with condition (*E stays, B moves* and *E moves, B stays*) and genus as factors on the percentage of movement. There was no significant effect for condition, $F(1,21) = 0.025$, $p = 0.88$, or genus, $F(2,21) = 0.48$, $p = 0.62$, but there was a significant condition × genus interaction, $F(2,21) = 4.13$, $p = 0.031$. Post-hoc analyses revealed that chimpanzees moved more when the experimenter rather than the bowl moved (p = 0.017). Gorillas (p = 0.13) and orangutans (p = 0.78) did not move differentially depending on the manipulation, although gorillas seemed to follow the bowl rather than the experimenter.

Until now, we have focused on the movements that occurred from the ape's starting location to the opposite location around the experimental booth. However, in some trials subjects also moved to the back of the cage away from the experimental booth. To analyze whether there was an effect of condition on the percentage of movements to the back of the cage we conducted a 4×3 ANOVA with condition as within-subject factor and genus as between-subject factor on the percentage of movements to the back of the cage. There was a significant effect for condition, $F(3,63) = 6.71$, $p = 0.001$, and no effect for genus, $F(2,21) = 1.11$, $p = 0.35$, or condition × genus, $F(6,63) = 0.31$, $p = 0.93$. A post hoc pairwise comparison showed that subjects moved significantly more often to the back of the cage in the *E stays, B moves* condition (mean = 24.3% of the trials) compared to all other conditions (*E stays with B*: mean = 5.6%, p = 0.005; *E moves with B*: mean = 5.2%, p = 0.006). Similarly, subjects moved more often to the back of the cage in the *E moves, B stays* condition (mean=15.7% of the trials) compared to the *E moves with B* (p = 0.019) and approached significance for the *E stays with B* condition (p = 0.062). Finally, there were no significant differences between the two conditions in which the experimenter and the bowl stayed together (p = 0.91). Those results show that subjects were more likely to move to the back of the cage in those conditions, where the bowl and the experimenter were segregated. Thus, the experimenter was not in the position to give food without changing her position.
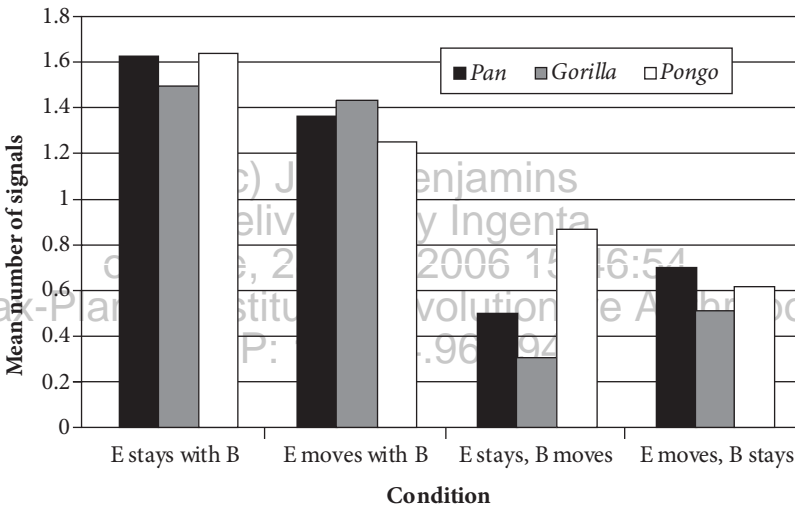
Signals

Table 2 shows for each signal its mean frequency depending on species. Chimpanzees and bonobos are shown separately, since they used different signals to beg for food. In general, the most frequent signals were visual signals, such as 'finger in hole' (N = 245) and 'mouth on hole (N = 80) followed by 'begging' (N = 50). Chimpanzees had the largest repertoire of all the species, in particular with visual and auditory signals. Orangutans also performed a wide range of visual signals, but like bonobos and gorillas they used a very low number of auditory signals.

Table 2. Mean frequency ± standard deviation (SD) depending on species and total frequency of each signal. For definitions of the signals, see Appendix 1.

|	Bonobo	Chimpanzee	Gorilla	Orangutan	Total Frequency
Visual signals					
arm raise	0.67 ± 1.16				2
begging		3.56±2.96	0.4±0.89	2.67±2.42	50
exchange			0.2±0.45	3.5±5.28	22
finger in hole	8±9.85	12.44±11.92	13.4±4.39	7±1.794	245
shake hand		0.22±0.44		1.17±2.40	9
head bob		0.56±1.13			5
lip flip		0.11±0.33			1
head on frame	0.33±0.58				1
mouth on hole	10±14	0.11±0.33	0.4±0.89	7.83±6.37	80
mouth on panel				0.5±1.23	31
rocking		0.11±0.33			1
stick through hole			1±1.41	0.67±1.21	9
Tactile gestures					
pull		0.22±0.67			2
touch	1.67±2.89	2.56±4.83	0.6±1.34	0.17±0.41	32
touch with object			0.4±0.55		2
Auditory signals					
hand clap		0.89±2.67			8
flip panel		0.33±0.5			3
jump against panel	0.33±0.58				1
knock		3.67±5.03	0.2±0.45		34
spit		0.22±0.67		1.83±2.56	13
vocalizations		2±4.92		0.33±0.82	22

Figure 4 shows the mean number of signals as a function of genus and condition. A 4×3 ANOVA with condition as within-subject factor and genus as between-subject factor on the number of signals indicated a significant effect for condition, $F(3,63) = 20.76$, $p < 0.001$, and no effect for genus, $F(2,21) = 0.06$, $p = 0.94$, or condition × genus, $F(6,63) = 0.60$, $p = 0.73$. A post hoc pairwise comparison showed that subjects signaled more often in those conditions in which the bowl and the experimenter stayed together compared to those in which they were split ($p < 0.001$ in all cases). Moreover, there were no significant differences between conditions in which experimenter and bowl stayed together ($p = 0.14$) or were split ($p = 0.63$).

Figure 4. Mean number of signals used per condition shown for each genus.
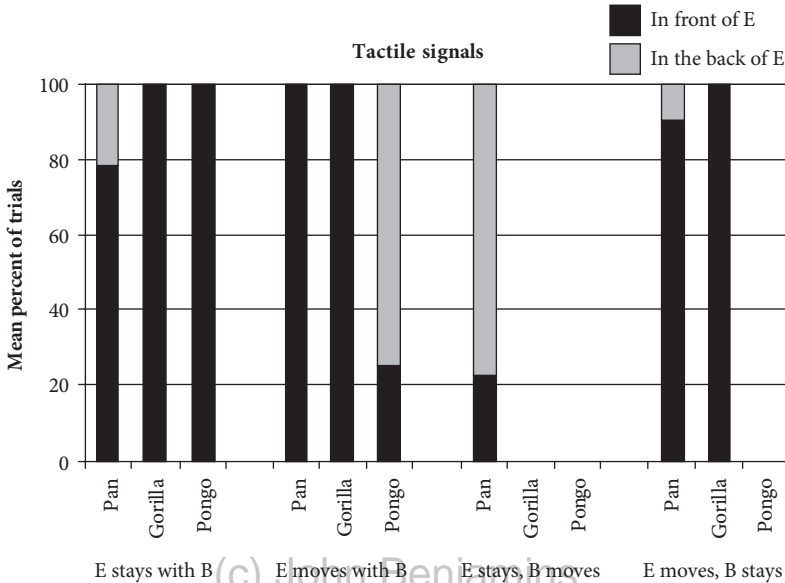
Figure 5 shows for each condition the mean percentage of trials in which visual gestures were performed in front as opposed to the back of the experimenter. Chimpanzees and bonobos produced visual gestures preferentially in front of the experimenter in all conditions. Gorillas also did so except in the condition in which the experimenter moved but the bowl stayed on the same side as the ape. In particular, gorillas and orangutans produced only 37.5 % and 52.8 %, respectively, of their visual gestures in front of the experimenter in this condition. A 4×3 ANOVA with condition and genus as factors on the percentage of visual gestures indicated a significant effect of condition, $F = (3,30) = 8.772$, $p < 0.001$ and genus × condition interaction ($F(6,30) = 2.76$,

p=0.029), but no effect for genus, F=(2,10)=1.673, p=0.236. Post-hoc analyses revealed no significant differences between genera in the first three conditions depicted in Figure 5 (p≥0.269). In contrast, there were significant differences between genera in the condition in which the experimenter moved without the bowl (p=0.024). Thus, chimpanzees and bonobos produced significantly more visual signals in front of the experimenter than gorillas (p=0.008), but not orangutans (p=0.196). There was also a trend that orangutans used more visual gestures in front of the experimenter than gorillas (p=0.059). Nevertheless orangutans performed visual gestures less often in front of the experimenter in this condition compared to those conditions in which the experimenter either stayed (p=0.029) or moved with the bowl (p=0.018). Similarly, gorillas performed significantly less visual signals in front of the experimenter in this condition compared to all other conditions (*E stays with B*: p=0.001; *E moves with B*: p<0.001; *E stays, B moves*: p=0.014).
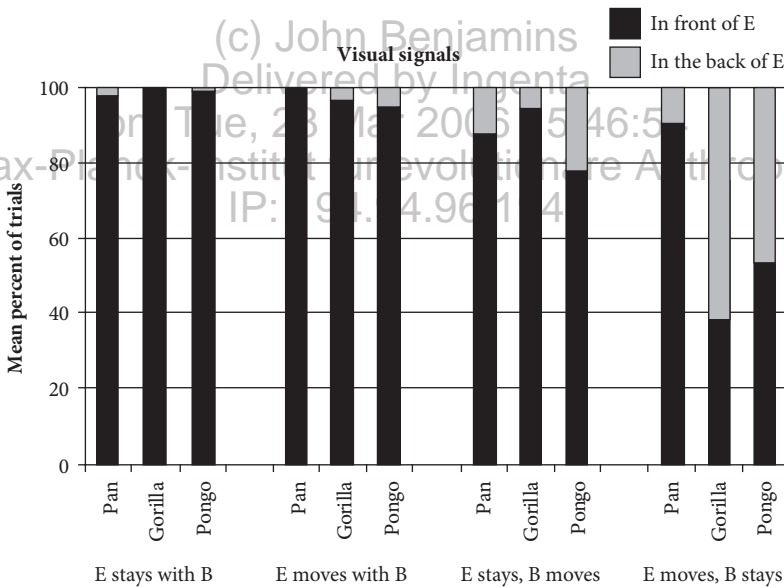
Figure 5. Use of visual signals depending on condition. For each genus the mean percent of signals performed in front of E compared to the percent performed in the back of E is shown.
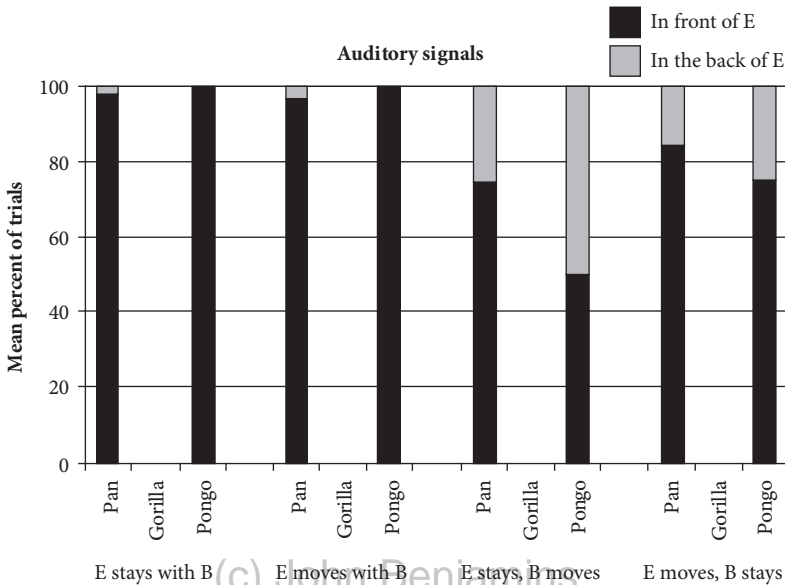
Figure 6 shows for each condition the mean percentage of trials in which tactile gestures were performed in front as opposed to the back of the experi-

Figure 6. Use of tactile signals depending on condition. For each genus the mean percent of signals performed in front of E compared to the percent performed in the back of E is shown.

menter. The missing data points for some genera in some conditions precluded us from conducting the corresponding ANOVA. Nevertheless, a visual inspection of Figure 6 indicates that *Pan* and *Gorilla* performed their tactile gestures in front of E even when they had to move from their starting position. This suggests that they did not use tactile gestures to call the experimenter's attention in case her back was turned.

Figure 7 shows for each condition the mean percentage of trials in which auditory gestures were performed in front as opposed to the back of the experimenter. Gorillas did not produce any auditory signals, therefore we concentrated the analyses on the other two genera. A 4×2 ANOVA with condition and genus as factors on the percentage of auditory gestures found no significant effect of condition, $F = (3,9) = 3.29$, $p = 0.72$, genus, $F = (1,3) = 2.75$, $p = 0.20$, or condition × genus, $F = (3,9) = 1.35$, $p = 0.32$. Thus, we found no difference in the way *Pan* and *Pongo* deployed auditory signals as a function of the orientation of the experimenter.

Figure 7. Use of auditory signals depending on condition. For each genus the mean percent of signals performed in front of E compared to the percent performed in the back of E is shown.

Discussion

Faced with a human with her back turned and who is in possession of food, chimpanzees walk around to beg from this human rather than call attention to make her turn around and then beg from her. Even tactile and auditory signals that could be used to call the attention of a non-oriented recipient are nevertheless used preferentially once the subject has moved to a position in which the potential recipient can see her. Thus, when given a choice between moving around a potential food donor, and using tactile or auditory signals to make the donor move, chimpanzees prefer to move themselves so that their signals may be seen.

These results are not only representative of chimpanzee behavior; they also can be extended to the other three great ape species that we studied. Moreover, all species also used visual gestures preferentially when they were facing the experimenter in most conditions — a result that confirms previous studies on gestural use in apes (Liebal et al., 2004; Pika et al., 2003; Pika et al., in review; Tomasello et al., 1994, 1997). Despite the overall similarities among species, an intriguing difference among genera emerged in connection to the condition in

which the experimenter moved to the alternative location and left the bowl in place (behind her). In this condition, chimpanzees and bonobos differed from gorillas and orangutans in both their movement patterns around the booth and the deployment of their visual signals. First, chimpanzees and bonobos moved more often when the experimenter changed location (and the bowl remained in the same place) compared to when the bowl changed location (and the experimenter remained in the same place). This seems to indicate a special sensitivity for directing the visual signals to a human with the appropriate body orientation. This is particularly remarkable because subjects had to leave the place where the bowl with food was and move to the location where the human (without food) was sitting. In contrast, gorillas and orangutans did not move differentially across these two conditions. Second, chimpanzees and bonobos preferentially used visual gestures to the front of the experimenter in all conditions, whereas orangutans and, especially gorillas, failed to do this in the condition in which the human turned around leaving the food next to the subject. Again, this seems to indicate a greater sensitivity of the members of the genus *Pan* compared to the other two ape genera to the orientation of the humans when deploying visual gestures. This distinction between *Pan* and other ape species may indicate that *Pan* has refined its social cognitive abilities after the split of the common ancestor between *Pan* and *Gorilla*. Besides studies on mirror self-recognition (see Tomasello & Call, 1997, for a review) this is the first study that has uncovered a possible difference in social cognition among the great apes.

A further question is how these results relate to previous studies. On the one hand, the current data support the idea that segregating the experimenter from the food reduces the individuals' tendency to beg for the food. In this context, Kaminski et al. (in press) found that when apes were not oriented toward the position of food, they did not gesture differentially depending on whether the human had her face oriented to them. In contrast, they gestured differentially depending on face orientation if the human's body was also oriented to them. The authors interpreted these results as evidence that body and face orientation signal two different types of information: face orientation encodes the experimenter's perceptual access, whereas body orientation encodes the disposition to provide food. Further support for this idea is provided by the fact that subjects in the current study went to the back of the cage more often when the food and the experimenter were not together, presumably because they perceived that the human was not in a disposition to give food. Moreover, data on the mean number of signals used across condi-

tions further confirmed this result because more signals occurred when the human and the food were not dissociated. Note that this behavior also contradicts the notion that subjects simply signal due to the presence of food or the presence of the experimenter because both (the food and the experimenter) remained in the room throughout the experiment.

On the other hand, this study differs from the results found by Hostetter et al. (2001) because unlike that study apes in the current study did not use signals to call attention. However, apes in the setup of Hostetter et al. (2001) were more limited in the options that they had available because they could not go around the experimenter. It is conceivable that if the apes in the current study were prevented from moving around, they may deploy more signals to get the attention of the human. Alternatively, the chimpanzees in the study of Hostetter et al. (2001) may have used the detour strategy rather than the attention getting strategy if offered the possibility to do so. Another explanation for this apparent discrepancy between studies is that auditory information in the study of Hostetter et al. (2001) did not function as an attention modifier per se, but as a signal that is deployed when a direct visual connection between individuals is prevented. Thus, the function of auditory and tactile signals is not to modify an attentional state but instead they are signals that are transparent in meaning, and depending on the state of the recipient they are deployed accordingly. Future studies will have to see if this distinction has any merit.

Note

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Appendix 1: Definitions of signals (shown in alphabetical order).

Signal	Definition
arm raise	Subjects raises arm as if to hit
begging	Subject puts finger(s) or hand through the hole of the panel with the palm upwards
exchange	Subject passes remaining food items through the hole
finger in hole	Subject puts its finger(s) or hand through the hole of the panel with the palm downwards
flip panel	Subject puts its fingers in the hole and pulls on it
hand clap	Subject slaps both hands together
head bob	Subject 'bobs and weaves' its head
head rest	Subject puts its head on the frame of the panel with the mouth closed while gazing at E
jump against panel	Subject kicks the panel with one foot or both feet
knock	Subject knocks at the panel or mesh with its knuckles, back of the hand or wrist
lip flip	Subject puts its mouth in the hole or at the panel with the upper lip flipped upwards
mouth on hole	Subject puts its open mouth into the hole of the panel
mouth on panel	Subject puts its open mouth on the panel (not in the hole)
pull	Subject pulls on the experimenter
rocking	Subject moves its upper body repeatedly back and fro
shake hand	Subject moves one hand or both around the wrist
spit	Subject spits at the experimenter
stick through hole	Subject puts a stick through the hole without touching the experimenter
touch	Subject touches the experimenter with its one hand or both
touch with object	Subject touches the experimenter with a stick
vocalizations	Vocal utterances directed toward the experimenter to obtain food

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