

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/49778144>

# Focus on the essential: All great apes know when others are being attentive

Article in *Animal Cognition* · May 2011

DOI: 10.1007/s10071-011-0378-5 · Source: PubMed

CITATIONS

47

READS

103

3 authors:



**Sebastian Tempelmann**

Bern University of Teacher Education

26 PUBLICATIONS 182 CITATIONS

[SEE PROFILE](#)



**Juliane Kaminski**

University of Portsmouth

87 PUBLICATIONS 3,217 CITATIONS

[SEE PROFILE](#)



**Katja Liebal**

Freie Universität Berlin

123 PUBLICATIONS 2,376 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



General Studies Education (Nature, Humans, Society) [View project](#)



The origins of gestures and language [View project](#)

# Focus on the essential: all great apes know when others are being attentive

Sebastian Tempelmann · Juliane Kaminski ·  
Katja Liebal

Received: 18 April 2010/Revised: 21 December 2010/Accepted: 2 January 2011/Published online: 22 January 2011  
© Springer-Verlag 2011

**Abstract** When begging for food, all great ape species are sensitive to a human's attention. However, studies investigating which cues are relevant for chimpanzees to assess the attentional state of others have produced highly inconsistent results. Some have suggested chimpanzees differentiate attention based on the status of the face or even the eyes, while others have indicated that body posture alone is the relevant cue. Kaminski et al. (Anim Cogn 7:216–223, 2004) compared the behaviour of chimpanzees, bonobos and orangutans while begging for food from a human experimenter who systematically varied his face and body orientation. Their results indicated that both factors, face and body orientation, affect apes' begging behaviour. The authors claimed that while body orientation provides information about the experimenter's general disposition to offer food, the visibility of the face provides information about the human's attentional state. In the current study, we tested this hypothesis with all four great apes species. However, unlike Kaminski et al. (Anim Cogn 7:216–223, 2004), the experimenter was able to hand over food regardless of body orientation. The results show that as soon as the offering of the food was no longer restricted, the orientation of the face became the key factor.

Therefore, we present the first evidence that all great ape species are able to assess the attentional state of a recipient based on the orientation of the face.

**Keywords** Communication · Attentional state · Referential communication · Great apes · Requesting behaviour · Triadic communication

## Introduction

Being able to assess another's attentional state during social interactions is an important skill, particularly in communicative interactions involving visual signals. Only if the other individual is attending will the visual signal be successful. Even though a large body of research has investigated non-human apes' abilities in this domain, the findings are somewhat inconsistent in terms of which cues the subjects actually attend to. From observational studies, focusing on communicative interactions between conspecifics, there is evidence that all great ape species adjust their communication depending on the body posture of potential recipients. That is, they use visual signals only when a recipient is facing them or they even move within the recipient's visual field (for chimpanzees: Liebal et al. 2004a; Tomasello et al. 1994, 1997; for bonobos: Pika et al. 2005; for gorillas: Genty et al. 2009; Pika et al. 2003; for orangutans: Liebal et al. 2006; Tempelmann and Liebal 2009).

Several experimental studies have been conducted in order to further analyse just how flexible apes' understanding of another's attentional state is and which cues must be attended in order to determine it. One paradigm used extensively is the so-called requesting paradigm. The subject is positioned opposite one or several human

---

S. Tempelmann (✉) · K. Liebal  
Department of Educational Science and Psychology,  
Freie Universität Berlin, Berlin, Germany  
e-mail: tempelmann@eva.mpg.de

S. Tempelmann · J. Kaminski · K. Liebal  
Department of Developmental and Comparative Psychology,  
Max-Planck Institute for Evolutionary Anthropology,  
Leipzig, Germany

S. Tempelmann · K. Liebal  
University of Portsmouth, Portsmouth, UK

experimenters whose attentional states vary. The question being explored is whether the subject will adjust its begging behaviour to the attentional state of the human and/or is able to assess who to beg from. One of the first researchers to use this paradigm were Povinelli and Eddy (1996) who presented chimpanzees with a choice of two humans. In a series of conditions, both experimenters engaged in different attentional states, e.g. one human was oriented towards the chimpanzee, while another faced away from it. Results indicated that the chimpanzees made their choice of who to beg from based on body orientation rather than the orientation of the face or the status of the eyes. Povinelli and colleagues therefore concluded that chimpanzees know virtually nothing about the role of the eyes (or the role of face orientation) in terms of perception.

Nevertheless, it accumulates evidence suggesting that at least chimpanzees differentiate a human's attention based on the status of the human's eyes. Call and Tomasello (1994) and Gomez (1996) found that chimpanzees (and also some enculturated orangutans) were sensitive to the status of a human's eyes (see also Kaminski et al. 2004). Also Hostetter et al. (2007) were able to demonstrate that chimpanzees tested in the requesting paradigm attended to the status of the eyes, in as much as the apes used auditory gestures more frequently when the human's eyes were closed compared to when they were open. In Povinelli et al.'s study (2003), chimpanzees adjusted their communicative behaviour depending on a human experimenter's attentional state; that is, depending on where the human was looking (e.g. the relevant food or the ceiling).

Chimpanzees (other species are underrepresented in the aforementioned studies) therefore seem to be quite flexible in their understanding of another's attentional state, an ability which seems to be grounded on a true understanding of another's visual perspective (e.g. Hare et al. 2000, 2001; Okamoto-Barth et al. 2007). Therefore, these results are contradictory to Povinelli et al.'s findings and conclusions. A recent study of Kaminski et al. (2004) incorporating different ape species (bonobos, chimpanzees and gorillas) has begun to provide the first findings that might help to clarify this antagonism and draw conclusions about the factors that influence other ape species' assessment of a human's attentional state. In that study, using the requesting paradigm, the experimenter's attentional state was varied systematically by manipulating two factors that might potentially influence the apes' behaviour; the orientation of the human's face and the orientation of the human's body. The apes begged a human for food who was engaged in one of four possible face and body orientations, which varied independently. Contrary to Povinelli and Eddy (1996), subjects were only presented with one experimenter; thus, the experimental manipulation took place across trials. Interestingly, the authors found an

interaction between the two main factors, face and body orientation, suggesting that both factors affected the apes' communicative behaviour. When the experimenter was bodily oriented towards the subject, the apes attended to the orientation of the face and begged more when it was oriented towards them than away from them. However, when the experimenter was oriented away from them, this effect vanished and the orientation of the face no longer affected the apes' begging behaviour. Indeed, the apes begged significantly less when the experimenter was oriented away from them. Kaminski et al. (2004) suggest that this may be the result of body and face orientation conveying two different types of information and a bivariate and hierarchical interpretation of the two factors. While body orientation may impart information about the experimenter's general ability to hand over food, face orientation provides information about the experimenter's actual attentional state. If this were the case, apes should only attend to the orientation of the face when the human experimenter is in a position to hand over food, regardless of body orientation. Furthermore, the authors could not detect any species difference regarding these findings.

In the current study, we tested Kaminski et al.'s hypothesis systematically by eliminating the apes' need to pay attention to the human's body orientation. We did so by using a feeding device with which the experimenter was able to deliver food independently of his body orientation. However, little is known about how the other ape species assess humans' attentional states which makes it difficult to make statements about the evolution of this ability. Therefore, we also compared all great apes species systematically with the same paradigm.

## Method

### Subjects

Six orangutans (*Pongo pygmaeus*), four gorillas (*Gorilla gorilla*), 18 chimpanzees (*Pan troglodytes*) and five bonobos (*Pan paniscus*) participated in this experiment. There were 23 females and 10 males ranging in age from 4 to 35 years. Fourteen apes were human reared, 17 were mother reared, and the rearing history of two individuals was unknown. With one exception, all subjects were born in captivity (see Table 1 for an overview).

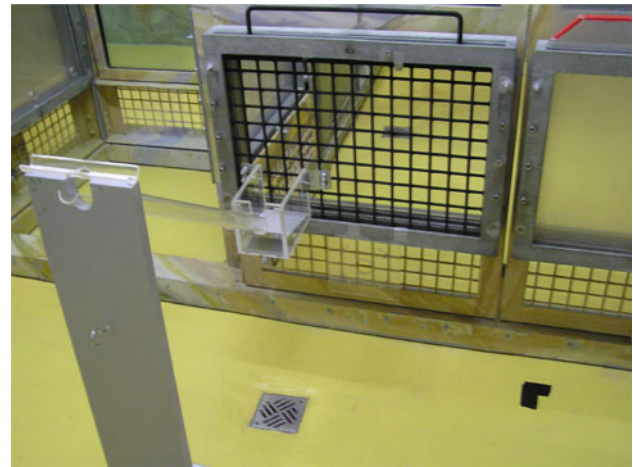
All apes were housed at the Wolfgang Köhler Primate Research Centre at Leipzig Zoo (Germany), where they lived in groups of conspecifics. All apes had access to indoor and outdoor areas. During testing, the apes were fed according to their daily routine four times a day on a diet of fruit, vegetables and monkey chow; water was available ad libitum.

**Table 1** Details of the subjects participating in the present study

Name	Species	Gender	Age	Rearing	Place of birth
Tai	Chimpanzee	Female	6	Mother reared	Captivity
Lome	Chimpanzee	Male	7	Mother reared	Captivity
Pia	Chimpanzee	Female	9	Mother reared	Captivity
Alex	Chimpanzee	Male	7	Human reared	Captivity
Alexandra	Chimpanzee	Female	9	Human reared	Captivity
Annett	Chimpanzee	Female	9	Human reared	Captivity
Patrick	Chimpanzee	Male	11	Mother reared	Captivity
Frodo	Chimpanzee	Male	14	Mother reared	Captivity
Sandra	Chimpanzee	Female	15	Mother reared	Captivity
Jahaga	Chimpanzee	Female	15	Mother reared	Captivity
Trudi	Chimpanzee	Female	15	Mother reared	Captivity
Dorien	Chimpanzee	Female	27	Human reared	Captivity
Natascha	Chimpanzee	Female	28	Human reared	Captivity
Riet	Chimpanzee	Female	30	Human reared	Captivity
Corrie	Chimpanzee	Female	31	Human reared	Captivity
Ulla	Chimpanzee	Female	31	Human reared	Captivity
Fraukje	Chimpanzee	Female	32	Human reared	Captivity
Robert	Chimpanzee	Male	32	Human reared	Captivity
Yasa	Bonobo	Female	11	Mother reared	Captivity
Ulindi	Bonobo	Female	15	Mother reared	Captivity
Kuno	Bonobo	Male	12	Human reared	Captivity
Limbuko	Bonobo	Male	13	Human reared	Captivity
Joey	Bonobo	Male	26	Human reared	Captivity
Kila	Orangutan	Female	8	Mother reared	Captivity
Padana	Orangutan	Female	11	Mother reared	Captivity
Dokana	Orangutan	Female	19	Mother reared	Captivity
Pini	Orangutan	Female	20	Mother reared	Captivity
Dunja	Orangutan	Female	35	Mother reared	Captivity
Bimbo	Orangutan	Male	28	Unknown	Captivity
Kibara	Gorilla	Female	4	Mother reared	Captivity
Viringika	Gorilla	Female	13	Mother reared	Captivity
Gorgo	Gorilla	Male	27	Human reared	Captivity
Bebe	Gorilla	Female	29	Unknown	Wild

## Apparatus

The apparatus (see Fig. 1) consisted of one half of a dissected piece of transparent pipe (length: 20 cm) with a centred hole halfway along its length. This pipe was fixed to the uppermost edge of a tall upright board (height: 102.5 cm, width: 20 cm) so that the concave inner of the pipe acted as a receptacle. The board had a segment hewn directly beneath the hole in the Perspex pipe. Attached to the hole on the underside of the pipe was a transparent tube (length: 69.5 cm, diameter: 4 cm) which acted as a chute, carrying rewards from the open pipe at the top of the board down to a Plexiglas box, which was located 58.5 cm from the board. The Plexiglas box (height: 16.5 cm, depth:

**Fig. 1** Apparatus and general experimental setup

20 cm, width: 14.3 cm) was fixed at a height of 47.5 cm from the ground to a metal mesh. This mesh constituted the direct boundary of the apes' cage. The side of the box that was fixed to the mesh was open, allowing a subject to reach with its fingers into the box.

The experimenter sat next to the apparatus (see Fig. 1). The design of the apparatus enabled the experimenter to deposit food pieces into the open pipe (which shall henceforth be called the "platform") in full view of the subject. By pushing the food into the hole in the platform, the food made its way down the tube into the box beside the ape's enclosure.

## Warm up

The warm up ensured that the subjects understood the mechanism of the apparatus and that the experimenter was able and willing to give them food independent of his body position. The experimenter offered food (approximately every 10 s) by pushing it through the tube in the apparatus. The experimenter changed his body position randomly in order to show subjects that food could be given irrespective of body orientation. Each individual received a warm up at the beginning of each testing day (for 2 min) and between sessions (for 1 min).

## Experimental procedure

E sat beside the apparatus and in front of the subject. During the experimental trials, E placed a piece of food on the platform in front of the subject and engaged in one of 4 possible conditions (modelled after Kaminski et al. 2004).

1. *Face/Front*: E's body and face were oriented towards the subject.
2. *No face/Front*: E's body was oriented towards the subject, while his head was turned away from the subject.

3. *Face/Back*: E's body was turned away from the subject, and his face was oriented towards the subject.
4. *No face/Back*: E's body and face were turned away from the subject.

During each trial, E remained motionless, holding the respective position for 30 s. Subsequently, without changing his body orientation, E dropped the food through the tube where it travelled to the subject. To keep subjects motivated to beg for the food, one to four filler trials followed each experimental trial. During the filler trials, E placed some food on the platform and offered it to the subject immediately, without waiting for any requesting behaviour.

Each subject received four session (2 sessions per day), with 4 trials per session resulting in up to 16 trials altogether. Each condition was presented once in each session, and order of condition was randomized across sessions. There was a break of approximately 1 min between the consecutive sessions of a day, during which time the experimenter left the testing room.

#### Data scoring

All experimental trials were video-recorded from three different perspectives, using a splitter, and were later coded by a second person. Opposed to Kaminski et al. (2004), who coded only five different behaviours, we coded the complete set of subjects' behaviour using a deductive/inductive coding schema; this had several reasons. Different from Kaminski et al.'s (2004) setting, we used a mesh instead of a Plexiglas panel, between experimenter

and subject; this gave subjects a little more degrees of freedom, which is why we could code behaviour that Kaminski et al. (2004) could not find, like "mesh shake". We also looked detailed at the different modalities of signals (e.g. visual and auditory signals) and whether there was a differential use of these modalities depending on the human's attentional state; thus, we included the complete set of signals used by the individuals.

For analysis, we grouped behaviour into three different categories depending on their modalities; these were unimodal visual, unimodal auditory and bimodal visual–auditory signals (see Table 2 for definitions).

#### Reliability

For inter-observer reliability, roughly 20% of the video material was coded by a person unfamiliar with the hypothesis of the study. Reliability was excellent (Spearman  $r = 0.82$ ,  $P < 0.001$ ,  $n = 93$ ).

#### Results

To analyse whether the subjects' behaviour differed between the four sessions, we conducted an ANOVA with the within factors condition and session and the between factor species. Analyses revealed that for all species, the factor session had no influence on the total number of behaviours in the respective condition. Therefore, for the following analyses, we pooled the data of all (four) trials for each respective condition.

**Table 2** Definition of signals in the current study classified according their respective sensory modality

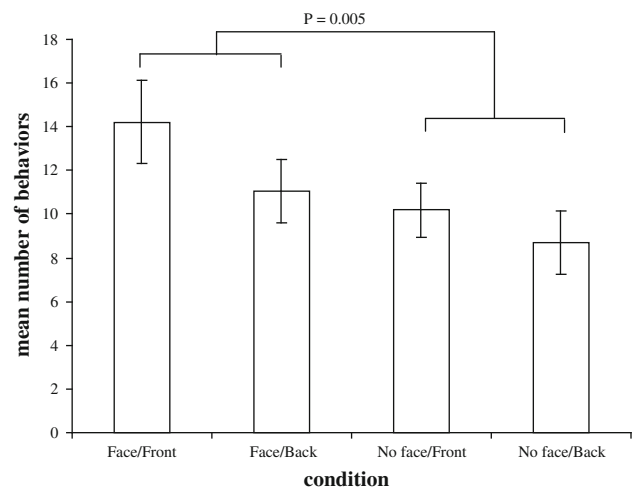
Signal modality	Definition
Unimodal visual	Produced with the limbs or the face and not audible for a recipient
Poke	Insertion of at least one finger or toe through the mesh
Present mouth	Pressing the mouth against the mesh or presentation of pursed lips
Trade object	Slipping of an object through the mesh
Swagger	Rocking of the body from side to side
Hand shake	Repeated shaking of one or both hands
Bimodal visual–auditory	Produced with the limbs or the face and audible for a recipient
Scratch	Scratching the mesh with the fingers
Mesh shake	Adherence of the mesh with hand or feet and coincidental back and forth movement
Hit	Hitting the side wall or mesh (without the insertion of the fingers/toes)
Spit	Spitting through the mesh
Clap	Hands or feet are clapped together
Ground slap	Slapping the ground with one hand or both or one foot
Jump	Jumping with both feet off the ground
Unimodal auditory	Vocalizations
Vocalization	Production of vocal sounds

## Unimodal visual signals

First, we focused on the apes' performance with regard to unimodal visual signals (see Table 3). These signals are especially interesting in the present context, because their adequate usage postulates an assessment of a potential recipients' attentional state on the basis of their visual perspective. We conducted an ANOVA with the within factors body orientation (front vs. back), face orientation (towards vs. turned) and the between factor species. It revealed a significant effect of face orientation ( $F_{1, 29} = 9.147$ ,  $P = 0.005$ ) with subjects producing more gestures when the experimenter's face was oriented towards them rather than turned away (see Fig. 2). There was no interaction with the factor body ( $F_{1, 29} = 0.621$ ,  $P = 0.44$ ) or with the between factor species ( $F_{3, 29} = 2.427$ ,  $P = 0.085$ ). Body orientation had no main effect ( $F_{1, 29} = 1.849$ ,  $P = 0.184$ ); however, there was an interaction with species ( $F_{3, 29} = 5.593$ ,  $P = 0.004$ ). A post hoc comparison revealed that overall chimpanzees produced more unimodal visual signals ( $M = 27.50$ ;  $SD = 18.87$ ), when the front of the experimenter's body was orientated towards them, compared to when E presented his back ( $M = 18.94$ ;  $SD = 17.28$ ; Wilcoxon test,  $z = -3.466$ ,  $P = 0.001$ ). No other factors or their interaction had a significant effect.

## Unimodal auditory and bimodal visual–auditory signals

Second, we analysed the use of unimodal auditory signals and bimodal visual–auditory signals (see Table 2). Analyses were made regarding (1) their proportional use as initial signals (see Table 4 for mean values) and (2) their overall frequency (see Table 3). An ANOVA with the within factors body orientation (front vs. back), face orientation (towards vs. turned) and the between factor species revealed no significant effect of any one of the factors ( $F_{1, 29}$ ; all  $P$  values  $> 0.05$ ) or their interaction ( $F_{3, 29}$ ; all  $P$  values  $> 0.05$ ). This is true for unimodal auditory signals (vocalization) as well as bimodal (visual–auditory) signals, and both types of signals grouped together, independent of whether their proportional use as initial gestures, or their overall frequency, was analysed.



**Fig. 2** Mean number of unimodal visual signals (SE) produced by subjects across conditions

## Discussion

The current study shows that for the bonobos, gorillas and orangutans, the experimenter's face orientation was the only relevant factor helping them to assess the human experimenter's attentional state. This indicates that as soon as the experimenter is in a position to offer food, from whatever position, his body orientation no longer affects the subjects' behaviour. The results for the chimpanzees, however, are slightly different. While the face was also the major factor for them, the experimenter's body orientation also affected their behaviour. However, there was no interaction between both factors. Contrary to the findings of Kaminski et al. (2004) showing a hierarchal, bivariate relation between both factors in the current study, face and body orientation influenced chimpanzees' behaviour independently of each other.

At this point, we can only speculate why chimpanzees behaved differently to the other great apes. Compared to other great ape species, chimpanzees have a more pronounced competitive group structure. Chimpanzees have a less egalitarian (i.e. Boesch et al. 2002) and more aggressive (Furuichi 1997) social system than bonobos. Most interesting in this context, chimpanzees are reported to have less relaxed feeding competition (e.g. Kano 1992),

**Table 3** Mean number of signals of each modality produced in all trials of each respective condition (SD)

Signal modality	Mean number of signals per condition			
	Face/front	No face/front	Face/back	No face/back
Unimodal visual	14.21 (10.98)	10.18 (7.00)	11.06 (8.27)	8.70 (8.42)
Bimodal visual–auditory	1.67 (5.89)	2.06 (7.13)	1.67 (5.38)	1.45 (4.52)
Unimodal auditory	2.58 (7.01)	1.09 (2.60)	1.48 (4.05)	1.67 (5.15)
Unimodal auditory + Bimodal visual auditory	4.24 (9.84)	3.15 (7.86)	3.15 (6.78)	3.12 (6.66)

**Table 4** Mean proportion of initially produced signals per condition (SD)

Signal modality	Mean proportion of initial signals per condition			
	Face/front	No face/front	Face/back	No face/back
Bimodal visual–auditory	8.06 (22.56)	7.06 (21.25)	9.85 (23.72)	12.12 (28.04)
Unimodal auditory	0.76 (4.35)	0.76 (4.35)	3.27 (9.03)	1.52 (6.06)
Unimodal auditory + Bimodal visual auditory	8.82 (22.70)	7.82 (21.43)	13.12 (24.03)	13.64 (28.70)

and Hare et al. (2007) could experimentally demonstrate that they exhibit less social tolerance and are less cooperative during cofeeding compared to bonobos. Therefore, because chimpanzees in general potentially have to judge other group members' attentional states more directly and simultaneously (i.e. to avoid punishment or to have faster access to resources), it might be beneficial for them to use less exact but faster deductible features as initial indications of other individuals' attentional states.

However, our results clearly show that by removing the human's restriction on offering food, it removed the dominating effect of body orientation. However, this also supports the hypothesis that body and face orientation are indeed interpreted hierarchically and that the apes' attention to body orientation may mask their sensitivity to the experimenter's attentional state. This explains the contradictory results of studies where the experimenter's body orientation varied as opposed to other studies where it did not.

That apes assessment of the experimenter's ability to hand over food may mask their sensitivity to a human's attention becomes apparent when we compare two recent studies. Hostetter et al. (2007) found that chimpanzees, tested in the requesting paradigm, not only use a human's face as a relevant cue but also attend to the status of the eyes and distinguish between those situations where the experimenter's eyes are closed from situations where the experimenter's eyes are open. Kaminski et al. (2004), however, found no such effect for chimpanzees specifically or for the other great apes. The important difference between both studies may be that Kaminski et al. (2004) placed the food on a table between the ape and the experimenter, whereas in the Hostetter et al. (2007) study, the food was offered directly from the experimenter's hand. In line with our hypothesis, the apes' assessment of the experimenter's body orientation, and evaluation of E's ability to give them food, may mask their attention to the human's attentional state in one study but not in the other. This hypothesis is also supported by the findings of Hattori et al. (2009) who found that capuchin monkeys are sensitive to the state of a human's eyes in a requesting paradigm, but only when the desired food was offered directly from the human's hand, not when the food was placed on a table next to the experimenter.

Altogether, these findings might also indicate apes' problems to cope with triadic contexts in which they have to refer to a third entity (the food). That is, the recipient and the food have to be closely linked such that the communication towards the human automatically implies the delivery of food. In this sense, the communicative situation is reduced to a mainly dyadic context where it is sufficient to attract the human's attention towards the self, as the human's behavioural spectrum is reduced to food delivery. Further studies will be necessary to investigate apes' behaviour in triadic contexts investigating both their production and comprehension of signals (see also Gomez 2005).

The present findings also demonstrate that all great ape species are able to differentiate a human's attention on the basis of the orientation of the face. Thus, they suggest that the ability to assess other individuals' attentional states via the orientation of the face might represent a skill already present in the last common ancestor of the great apes. This finding is especially interesting since great apes' skills differ, especially with regard to the more sophisticated cognitive skills of visual perspective taking. For example, compared to gorillas, chimpanzees, bonobos and orangutans are less skilled at using a human's gaze as a referential cue (Okamoto-Barth et al. 2007). From the present study, we can conclude that this difference between the great ape species is not grounded in a general inability of orangutans to adequately assess other individuals' attentional states. A further finding of the present study was that apes did not use bimodal visual–auditory and unimodal auditory signals differentially depending on the attentional state of the recipient; namely, they did not use them more frequently when the human was not attending visually. This is supported by other studies using the food requesting paradigm (Kaminski et al. 2004; Liebal et al. 2004b), but also from observations of interactions of conspecifics (for chimpanzees: Liebal et al. 2004a; for orangutans: Tempelmann and Liebal 2009; for gorillas: Genty et al. 2009). Although chimpanzees and the other great apes use visual gestures preferentially when a conspecific or human is attending (e.g. Hostetter et al. 2001; Leavens et al. 2004, 2009); in the current study, they did not use unimodal auditory or bimodal signals to attract the attention of the human as other authors have concluded from their findings (e.g.

Hostetter et al. 2001, 2007; Leavens et al. 2004). However, we cannot say from where these differences stem. They may be due to the very large sample sizes used in these studies, which allowed the authors to detect significant behavioural differences that we could not identify.

In sum, by clearly signalling the human's ability and motivation to offer food to the subjects, we eliminated the dominating influence of body orientation on the apes' performance. As a consequence, the present study provides evidence that *all* great ape species judge a human's attentional state on the basis of what the face is doing (or even the eyes). Thus, the present study suggests that the ability to assess other individuals' attentional state via the orientation of the face constitutes a common skill in all great ape species and provides explanations for the seemingly contradictory results of previous studies following this paradigm. Furthermore, it demonstrates the necessity to take into account the triadic nature of the food requesting context.

**Acknowledgments** We would like to thank Martina Neumann and Laura Damerius for their help with coding the data and Nathan Pyne-Carter for the perusal of a former version of the manuscript and helpful comments. Many thanks to the keepers and administrative staff at the Wolfgang Koehler Primate Research Centre and to the Department of Developmental and Comparative Psychology at Max-Planck Institute for Evolutionary Anthropology in Leipzig. Sebastian Tempelmann and Katja Liebal are incorporated in the Project "Towards a grammar of gesture" founded by the Volkswagen—Stiftung, Germany. The reported experiments comply with all laws of the country in which they were performed.

## References

- Boesch C, Hohmann G, Marchant LF (2002) Behavioral diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge
- Call J, Tomasello M (1994) Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *J Comp Psychol* 108:307–317
- Furuichi T (1997) Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. *Int J Primatol* 18(6):855–875
- Genty E, Breuer T, Hobaiter C, Byrne RW (2009) Gestural communication of the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Anim Cogn* 12(3):527–546
- Gomez JC (1996) Non-human primate theories of (non-human primate) minds: some issues concerning the origins of mind-reading. In: Carruthers P, Smith PK (eds) *Theories of theories of mind*. Cambridge University Press, Cambridge, pp 330–343
- Gomez JC (2005) Requesting gestures in captive monkeys and apes: conditioned responses or referential behaviors? *Gesture* 5:91–105
- Hare B, Call J, Agnetta B, Tomasello M (2000) Chimpanzees know what conspecifics do and do not see. *Anim Behav* 59:771–785
- Hare B, Call J, Tomasello M (2001) Do chimpanzees know what conspecifics know? *Anim Behav* 61:139–151
- Hare B, Melis A, Woods V, Hastings S, Wrangham R (2007) Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Curr Biol* 17(7):619–623
- Hattori Y, Kuroshima H, Fujita K (2009) Tufted capuchin monkeys (*Cebus apella*) show understanding of human attentional states when requesting food held by a human. *Anim Cogn*. doi:10.1007/s10071-009-0248-6
- Hostetter AB, Cantero M, Hopkins WD (2001) Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional state of a human (*Homo sapiens*). *J Comp Psychol* 115:337–343
- Hostetter AB, Russell J, Freeman H, Hopkins WD (2007) Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention. *Anim Cogn* 10(1):55–62
- Kaminski J, Call J, Tomasello M (2004) Body orientation and face orientation: two factors controlling apes' requesting behavior from humans. *Anim Cogn* 7:216–223
- Kano T (1992) *The last ape: pygmy chimpanzee behavior and ecology*. Stanford University Press, Stanford
- Leavens DA, Hostetter AB, Wesley MJ, Hopkins WD (2004) Tactical use of unimodal and bimodal communication by chimpanzees (*Pan troglodytes*). *Anim Behav* 67:467–476
- Leavens DA, Russell JL, Hopkins WD (2009) Multimodal communication by captive chimpanzees (*Pan troglodytes*). *Anim Cogn*. doi:10.1007/s10071-009-0242-z
- Liebal K, Call J, Tomasello M (2004a) Use of gesture sequences in chimpanzees. *Am J Primatol* 64(4):377–396
- Liebal K, Pika S, Call J, Tomasello M (2004b) To move or not to move: how apes alter the attentional states of humans when requesting for food. *Interact Stud* 5:199–219
- Liebal K, Pika S, Tomasello M (2006) Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture* 6:1–38
- Okamoto-Barth J, Call J, Tomasello M (2007) Great apes understanding of others' line of sight. *Psychol Sci* 18:462–468
- Pika S, Liebal K, Tomasello M (2003) Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning, and use. *Am J Primatol* 60(3):95–111
- Pika S, Liebal K, Tomasello M (2005) Gestural communication in subadult bonobos (*Pan paniscus*): repertoire and use. *Am J Primatol* 65(1):39–61
- Povinelli DJ, Eddy TJ (1996) What young chimpanzees know about seeing. *Monogr Soc Res Child Dev* 61:1–152
- Povinelli DJ, Theall LA, Reaux JE, Dunphy-Lelii S (2003) Chimpanzees spontaneously alter the location of their gestures to match the attentional orientation of others. *Anim Behav* 66:71–79
- Tempelmann S, Liebal K (2009) The use of gesture sequences in orang-utans. *Folia Primatol* 80:144–145
- Tomasello M, Call J, Nagell K, Olguin R, Carpenter M (1994) The learning and the use of gestural signals by young chimpanzees: a transgenerational study. *Primates* 35:137–154
- Tomasello M, Call J, Warren J, Frost T, Carpenter M, Nagell K (1997) The ontogeny of chimpanzee gestural signals: a comparison across groups and generations. *Evol Commun* 1:223–253